Importance of floodplain waters for the conservation of chironomid (Diptera) biodiversity in a 6th order section of the Garonne river (France)

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Keywords : Diptera, Chironomidae, Garonne river, potamal, floodplain waters, biodiversity.

The chironomid populations of a 6th order section (400 m) of the middle Garonne river were studied monthly from September 1996 to October 1997.

For the first time the main channel of the river was investigated including two floodplain waters : a side arm and an oxbow. Two sampling techniques were used for drift and benthic collections. A total of 21 766 specimens (pupae and pupal exuviae) were sorted and 137 species were identified. Among these, 12 species are new for the fauna of France : their ecology and biogeography are given. The chironomid population of the backwaters is especially diverse and distinctive since the waterbody is disconnected from the main channel.

The studied section appears to be transitional corresponding with the epipotamal-metapotamal zones. The embankment of the watercourse since 1958, which has isolated floodplain waters and increased the current velocity in the main channel, mainly explains the dual typologic status observed. The main channel is colonised by rheophilous Orthocladiinae whereas the backwaters shelter a mixed population of limnophilous Chironominae and potamobiont Orthocladiinae.

This study demonstrates the urgency for preserving floodplain waters because of their species richness, their uniqueness and their faunal interaction with the main channel. The strong faunal contribution of floodplain waters highlights the topicality and the value in investigating the less disturbed potamal zones of large rivers to increase our knowledge on biodiversity, ecology and biogeography of chironomid populations.

Importance des annexes fluviales pour le maintien de la biodiversité des Chironomidés (Diptera) sur une section d'ordre 6 de la Garonne (France)

Mots-clés : Diptera, Chironomidae, Garonne, zone potamique, annexes fluviales, biodiversité.

Les peuplements de Chironomidés d'une section d'ordre 6 de la Garonne ont été suivis mensuellement de septembre 1996 à octobre 1997.

Pour la première fois, l'étude du chenal principal de la rivière inclue la prospection de deux annexes fluviales : un bras secondaire et un bras mort. Deux méthodes d'échantillonnage ont été utilisées : dérive de surface et prélèvement benthique. 21 766 spécimens (nymphe et exuvies nympheales) ont été dénombrés et 137 espèces identifiées. Parmi celles-ci, 12 sont nouvelles pour la faune de France : leur écologie et leur biogéographie sont précisées. Le peuplement chironomidien des annexes est d'autant plus diversifié et caractéristique que l'annexe est déconnectée du chenal principal.

La section de Garonne étudiée apparaît être une zone de transition correspondant à un épipotamal/métopotamal. L'enrochement du lit vif depuis 1958, qui a isolé les annexes fluviales et accru les vitesses d'écoulement dans le chenal principal, explique ce double statut typologique. Ainsi, le peuplement du chenal principal est dominé par des Orthocladiinae rhéophiles alors que les annexes fluviales présentent un peuplement mixte de Chironominae limnophiles et d'Orthocladiinae potamobiontes.

Cette étude montre la nécessité de préserver de telles zones annexes en raison de leur richesse, de leur spécificité et de leur interaction faunistique avec le chenal principal. La forte contribution faunistique des annexes fluviales souligne l'intérêt et l'actualité de prospecter les zones potamiques les moins perturbées des grandes rivières pour une meilleure connaissance de la biodiversité, de l'écologie et de la biogéographie des populations chironomidiennes.

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1. Introduction

The transverse dimension is one of the four dimensions identified within river hydrosystems (Ward 1989, Amoros & Petts 1993). This dimension includes the whole alluvial plain, defined as a mosaic of homogeneous patches on the physico-chemical and biological plan (Johnston & Naiman 1987, Pringle et al. 1988), as well as the transverse bi-directional exchanges controlling interactions within this mosaic (Amoros & Roux 1988, Junk et al. 1989, Bayley 1995).

This transverse dimension, dominant in potamal zones of the rivers, was the subject of numerous works synthesised by Amoros & Roux (1988). In Europe, in the first half of the XXth century, planning of rivers with the aim of commercial navigation and hydro-electric production involved the separation of the main channel from its alluvial plain (Walker 1985, Ward & Stanford 1986). The result was an alteration of the floodplain waters, which progressively filled in and disappeared (Amoros et al. 1987, Finlayson & Moser 1991, Ward & Stanford 1995b). However, the length of time that this takes allows the conservation of these zones within the large river systems and enables the study of their functioning, as for example, on the River Danube (Heiler et al. 1994 and 1995, Tockner & Bretschko 1996, Tockner et al. 1999), the Rhine and the Meuse rivers in the Netherlands (Van den Brink & Van den Velde 1991) or on the French Haut-Rhône (Amoros 1991, Castella et al. 1991, Cellot et al. 1994).

The ecological role of submersible lateral elements resulting from certain construction plans, such as the "caissons Girardon" of the Lower Rhône downstream of the city of Arles, and comparable to a certain extent to river backwaters, were also studied using several taxonomic groups (Fruget 1991, Franquet et al. 1995) or only chironomids (Franquet 1999).

In the Garonne river, remnant side arms and floodplain waters, permanently or temporarily connected to the main channel, are still functional between Toulouse (198 km from the source) and Castelsarrasin (275 km from the source) although this overflowing section was embanked since 1958. A study on the heterogeneity of the fluvial space and its biodiversity (Garcia 2000) has provided the opportunity to investigate those hydrogeomorphological components closely involved in the functioning of the hydrosystem, whereas, up to now, only the main channel of the Garonne river was investigated.

This paper presents the results of the floodplain waters investigation. Its purpose is to highlight the strong faunal interest of the alluvial zone of large rivers and

its importance in the conservation of the chironomid global biodiversity. The typological status of the embanked parts of large rivers is discussed.

2. Material and methods

2.1. Study area

The River Garonne flows for 575 km from the Massif of the Maladetta in the Spanish Pyrenees (alt. 1800 m) to the Gironde estuary, where the inter-annual mean daily discharge of the river is $630 \text{ m}^3 \cdot \text{s}^{-1}$. Its catchment area includes 56 000 km² of French territory. The substratum of the River Garonne in the study area is composed of mixed gravel and boulders laid on molasse, a waterproof formation of calcareous sandstone.

The sampling area is situated at Saint-Cassian, in a 6th order section according to Strahler's ordination method (Strahler 1952, 1964), 10 km downstream of Verdun-sur-Garonne (2 882 inh.) and 45 km downstream of the city of Toulouse (740 000 inh.) (Fig. 1). It is an embanked section, surrounded by agricultural land but preserved from other kinds of hydraulic development as well as from industrial or urban sources of pollution.

The four sampling sites cover a 400 metres long stretch of the river, selected upon consideration of the longitudinal and transverse heterogeneity of the potamal zone (Fig. 1). The sampling site called "Main channel" (MC) comprises a riffle (lotic zone) and an alluvial cove (lentic zone) in the left bank of the river. Two sampling sites (SA₁ and SA₂) are located in a side arm: SA₁, situated upstream, has fast flowing water generated by the narrowing of the stream; SA₂, situated downstream, is a lowland pool generated by the widening of the side arm. SA₁ is permanently connected to the main channel whereas SA₂ is temporarily connected. The lowland pool in the SA₂ site is associated with marginal shallow ponds isolated when the water level decreases. The sampling site called "Oxbow" (Ox) is situated in the downstream part of a long oxbow (1 200 m). It is submerged when the river's discharge is over $700 \text{ m}^3 \cdot \text{s}^{-1}$, which happens once a year. In terms of typology, the oxbow looks like a lowland muddy channel of standing water.

2.2. Sampling methods

The samples were taken monthly in the four sites from October 1996 to September 1997, using two sampling methods: drifting pupal exuviae (1) and benthic collections of pupae (2).

1) Collections of drifting pupal exuviae were taken using Brundin drift nets. A sub-sample of 500 exuviae was sorted and identified to species level. In the Garon-

MC : Main channel

SA₁ : Permanently connected side arm

SA₂ : Temporarily connected side arm

Ox : Oxbow

Fig. 1. Map of the study area and sample site locations. MC : Main Channel, SA₁ : Upstream side arm, SA₂ : Downstream side arm, OX : Oxbow.
Fig. 1. Carte du site étudié et localisation des stations. MC : Chenal principal, SA₁ : Bras secondaire amont, SA₂ : Bras secondaire aval, OX : Bras mort.

ne river, such a sub-sample size appeared suitable considering that, on average, 93% of the species richness is already obtained with about 400 exuviae (Fig. 2).

In general, authors have proposed various sizes of sub-samples to take, in order to obtain the best picture of the chironomid population. Some examples of this disparity are : Wilson & Bright (1973) took 200 exuviae in the River Rhine as well as Ruse (1993, 1995) in the Pang river. In the River Meuse, Kuijpers et al. (1992) as well as Evrard (1996) identified 300 pupal exuviae whereas Frantzen (1992) in the Lower Rhône river and Gendron & Laville (1995) in a 4th order section of the River Aude, showed that 500 exuviae was best.

It is obvious that the total number of species collected depends on numerous factors, natural - potential and real species richness of the site, hydrological connectivity of the floodplain... - and methodological ones - sampling period, number of samples, sampling duration...-. Thus, it is clear that the size of the sub-sample must be chosen according to the purpose of the study.

Biomonitoring studies use sub-samples of 200 - 300 specimens, providing useful information through frequent to dominant species. In the Meuse river, the probability of obtaining the frequent species was 95 %

with a sub-sample of 300 individuals (Evrard 1996). Conversely, faunal and biogeographic studies dealing with the biodiversity of hydrosystems and requiring the search for rare species will be more efficient with a sub-sample of 500 or even 600 pupal exuviae.

2) Benthic collections of pupae were taken using a Surber net (250 µm mesh size) at the micro-habitat scale. 12 types of substratum have been investigated : sand (0.5-2.5 mm), gravel (2.5-25 mm), boulders (25-75 mm), gravel-boulders, algae, submerged plants, emergent plants, roots, wood and mud, considering 3 classes of current velocity visually evaluated : standing water, slow flowing water and fast flowing water.

Pupae and pupal exuviae were identified especially using the keys to pupal exuviae of West Palaearctic Chironomidae (Langton 1991, 1995).

The two sampling methods appear fully complementary. The drift method allows an integrative and exhaustive collection of the species richness, suitable for biodiversity studies whereas the benthic method provides quantitative data on larval and pupal densities as well as information on micro-habitat associations for the species.

As regards specific composition of the community achieved by these two methods, drift samples provide

Fig. 2. Increase of species richness according to the size of the pupal skin sub-sample. Mean of the 43 drifts carried out in the Garonne River.

Fig. 2. Evolution de la richesse spécifique en fonction du nombre d'exuvies nymphales triées. Moyenne des 43 dérives effectuées sur la Garonne.

more rare species than benthic samples as seen by comparing drift and benthic abundance distributions of the species (Fig. 3). Nevertheless, the qualitative composition of the two populations are close as pointed out by the Kulczynski (1927) similarity index : $K=0.73$ (all species considered) and $K=0.86$ (rare species removed). The quantitative composition of the two populations are less close but stay similar ($K=0.60$).

3. Results

3.1. Checklist of chironomid species

From the 48 samples (4 sites x 12 dates), 17 747 pupal exuviae were collected by drift and 4 019 pupae by benthic collections. 130 species were recorded in the drift and 72 species in the benthic collections. Overall, 137 species distributed in 57 genera have been recorded (Table 1).

Among these, 12 species or taxa are new records for France according to check lists of the Diptera Chironomidae recorded in continental France and Corsica (Serra-Tosio & Laville 1991, Laville & Serra-Tosio 1996). This represents 9 % of the total species found in the sampling area :

- Orthocladiinae (6) *Corynoneurella paludosa* Brundin
Eukiefferiella Pe2 Langton 91
Limnophyes paludis Armitage
Parakiefferiella scandica Brundin
Thienemanniella Pe2a Langton 91
Thienemanniella Pe2b Langton 91
- Chironomini (2) *Chironomus riihimakiensis* Wülker
Cryptochironomus obreptans (Walker)
- Tanytarsini (4) *Paratanytarsus penicillatus* (Goetghebuer)
Tanytarsus buchonius Reiss & Fittkau
Tanytarsus nigricollis Goetghebuer
Tanytarsus recurvatus Brundin

These newly recorded species are rare species in the Garonne, except *Corynoneurella paludosa* and *Thienemanniella* Pe2a which respectively represent 0.6 % and 0.3 % of the total collections (Table 1).

Most of them are Palaearctic species widely distributed in Europe (Ashe & Cranston 1990). Nevertheless, it is interesting to note that 3 of them : *P. scandica*, *C. riihimakiensis* and *T. recurvatus*, are only known from Sweden, Norway and Finland. The River Garonne is the most southerly record for these 3 species.

Eukiefferiella Pe2 is only known from Czechoslovakia (Langton 1991) ; *C. obreptans* is widely distributed in Europe and in the ex-USSR ; *T. buchonius* is known

Fig. 3. Comparison of abundance distribution of species from drift and benthic data. Terminology according to Bournaud (1980).

Fig. 2. Comparaison de la distribution d'abondance des espèces obtenue en fonction des deux méthodes d'échantillonnage utilisées. Terminologie d'après Bournaud (1980).

Table 1. List of chironomid taxa found at Saint-Cassian, with their frequency. MC : Main channel, SA₁ : Upstream side arm, SA₂ : Downstream side arm, Ox : Oxbow.

Tableau 1. Liste des espèces de Chironomidés collectées à Saint-Cassian, et leur abondance relative au sein du peuplement. MC : Chenal principal, SA₁ : Bras secondaire amont, SA₂ : Bras secondaire aval, Ox : Bras mort.

			Drift Data					Benthic Data					Total	
			MC	SA ₁	SA ₂	Ox	Total	MC	SA ₁	SA ₂	Ox	Total	Nb	%
TANYPODINAE														
Ablabesmyia	longistyla	Fittkau				5	5						5	0.022
Conchapelopia	melanops	(Meigen)						1	3			4	4	0.018
Hayesomyia	tripunctata	(Goetghebuer)						1	1			2	2	0.009
Procladius	choreus	(Meigen)			44	19	63	1	1	17	1	20	83	0.381
Procladius	sagittalis	(Kieffer)			1		1						1	0.004
Psectrotanytus	varius	(Fabricius)				1	1		1			1	2	0.009
Rheopelopia	ornata	(Meigen)	2		2		4	16	8		1	25	29	0.133
Tanytus	punctipennis	(Meigen)		15	17	2	34	1		2		3	37	0.169
BUCHONOMYIINAE														
Buchonomyia	thienemanni	Fittkau	2				2						2	0.009
DIAMESINAE														
Pothastia	gaedii	(Meigen)	3	1	1	1	6			1		1	7	0.032
Pothastia	longimanus	Kieffer	6	2		1	9		2			2	11	0.050
PRODIAMESINAE														
Prodiamesa	olivacea	(Meigen)			27	6	33				1	1	34	0.156
ORTHOCLADIINAE														
Brillia	flavifrons	Johannsen	1			1	2						2	0.009
Brillia	modesta	(Meigen)	2				2	4				4	6	0.027
Bryophaenocladus	subvernalis	(Edwards)	1				1						1	0.004
Cardiocladius	fuscus	Kieffer	215	24	47		286	14	1			15	301	1.382
Corynoneura	carriana	Edwards			23	2	25				1	1	26	0.119
Corynoneura	celtica	Edwards	1				1						1	0.004
Corynoneura	gratias	Schlee			1		1						1	0.004
Corynoneura	lacustris	Edwards	11			3	14						14	0.064
Corynoneura	lobata	Edwards			1		1						1	0.004
Corynoneurella	paludosa	Brundin	54	43	4	1	102						102	0.468
Cricotopus	albiforceps	(Kieffer)	6	6	2	1	15						15	0.068
Cricotopus	annulatus	Goetghebuer	161	145	323	119	748						748	3.436
Cricotopus	bicinctus	(Meigen)	172	335	574	33	1 114	378	344	257	5	984	2 098	9.638
Cricotopus	curtus	Hirvenoja	18	15	57	80	170						170	0.781
Cricotopus	fuscus	(Kieffer)	38	119	144	1	302						302	1.387
Cricotopus	intersectus	(Staeger)	2			99	101	11	9	59	19	98	199	0.914
Cricotopus	similis	Goetghebuer	163	33	47		243	7	5			12	255	1.171
Cricotopus	sylvestris	(Fabricius)	9	14	194	305	522	130	22	218	133	503	1 025	4.709
Cricotopus	triannulatus	(Macquart)	29	45	47	1	122						122	0.560
Cricotopus	trifascia	Edwards	51	18	11	1	81	32	17	2		51	132	0.606
Cricotopus	vierriensis	Goetghebuer	167	92	182	6	447	15	9	5		29	476	2.186
Cricotopus (s.str.)	Pe2	Langton 91	1				1						1	0.004
Cricotopus	spp							126	186	62	11	385	385	1.768
Diplocladius	cultriger	Kieffer	2				2						2	0.009
Eukiefferiella	brevicalcar	(Kieffer)		1			1						1	0.004
Eukiefferiella	claripennis	(Lundbeck)	3	3	3		9	1				1	10	0.045
Eukiefferiella	clypeata	(Kieffer)	3	2	2		7						7	0.032
Eukiefferiella	devonica	(Edwards)	1				1						1	0.004
Eukiefferiella	ilkeyensis	(Edwards)	10	3	4		17		3			3	20	0.091
Eukiefferiella	lobifera	Goetghebuer	33	41	33		107		2			2	109	0.500
Eukiefferiella	pseudomontana	Goetghebuer	1				1						1	0.004
Eukiefferiella	Pe2	Langton 91							1			1	1	0.004
Limnophyes	paludis	Armitage				1	1						1	0.004
Limnophyes	punctipennis	(Goetghebuer)				1	1						1	0.004
Nanocladius	bicolor	Zetterstedt	6	14	4	5	29	3				3	32	0.147
Nanocladius	rectinervis	(Kieffer)	5	3	3	1	12				1	1	13	0.059
Orthocladius	ashei	Soponis	36	30	42	3	111	1	2			3	114	0.523
Orthocladius	carlatus	(Roback)	129	51	97	2	279	2	29	1		32	311	1.428
Orthocladius	lignicola	Kieffer	1	1			2	1	1			2	4	0.018
Orthocladius	oblidens	(Walker)	19	3	14	1	37		6	3		9	46	0.211
Orthocladius	pedestris	Kieffer	11	16	32	3	62	6	9	3		18	80	0.367
Orthocladius	rivicola	Kieffer	673	435	411	21	1 540	366	271	20	1	658	2 198	10.098
Orthocladius	rivulorum	Kieffer	4	8	2		14	1				1	15	0.068
Orthocladius	rubicundus	(Meigen)	2	6	6	1	15						15	0.068
Paracletus	conversus	(Walker)		6	44	10	60	1	3	15		19	79	0.362
Paracletus	niger	(Kieffer)	2				2						2	0.009
Parakiefferiella	scandica	Brundin			1		1						1	0.004
Parakiefferiella	smolandica	(Brundin)				2	2						2	0.009
Parametrioctonus	stylatus	(Kieffer)	6	3	1		10						10	0.045
Paratrichocladius	rufiventris	(Meigen)	44	39	52	18	153		10	1	2	13	166	0.762
Psectrocladius	oxyura	Langton				1	1						1	0.004
Psectrocladius	sordidellus	(Zetterstedt)				1	1						1	0.004
Rheocricotopus	chalybeatus	(Edwards)	1 069	91	79	6	1 245	30	18			48	1 293	5.940
Rheocricotopus	fuscipes	(Kieffer)	15	3	7	5	30		3		1	4	34	0.156
Synorthocladius	semivirens	(Kieffer)	2 387	1 187	964	68	4 606	95	81	22	1	199	4 805	22.076
Thienemanniella	Pe2a	Langton 91	1	23	25		49		2			2	51	0.234
Thienemanniella	Pe2b	Langton 91	2	3	2		7						7	0.032
Tveteria	calvescens	(Edwards)	323	23	20		366	9	6	2		17	383	1.759

Table 1. Continued.

Tableau 1. Suite.

			Drift Data					Benthic Data					Total	
			MC	SA ₁	SA ₂	Ox	Total	MC	SA ₁	SA ₂	Ox	Total	Nb	%
CHIRONOMINAE Chironomini														
Chironomus	spp							5	17	15	2	39	39	0.179
Chironomus	aprilinus	Meigen		2		11	13						13	0.059
Chironomus	bernensis	Wülker & Klotz	1		5	6	12						12	0.055
Chironomus	cingulatus	Meigen			1	8	9						9	0.041
Chironomus	commutatus	Keyl	3	21	341	68	433						433	1.989
Chironomus	longistylus	Goetghebuer				11	11						11	0.050
Chironomus	luridus	Strenzke				3	3						3	0.013
Chironomus	ruditanis	Keyl				2	2						2	0.009
Chironomus	obtusidens	Langton 95		2			2						2	0.009
Chironomus	plumosus	(Linnaeus)				1	1						1	0.004
Chironomus	riihimäkiensis	Walker				3	3						3	0.013
Chironomus	tenans	(Fabricius)			2	1	3						3	0.013
Cladopelma	virescens	(Meigen)	1	7	9	102	119						119	0.546
Cryptochironomus	obrepans	(Walker)			3	2	5						5	0.022
Cryptochironomus	rostratus	Kieffer	1	4	4		9			3		3	12	0.055
Cryptochironomus	supplicans	(Meigen)			1		1						1	0.004
Cryptotendipes	pseudotener	(Goetghebuer)			53		53						53	0.243
Cryptotendipes	usmaensis	(Pagant)						1	8	13		22	22	0.101
Cryptotendipes	Pelc	Langton 91		4	13	15	32						32	0.147
Demicryptochironomus	vulneratus	(Zetterstedt)			1		1						1	0.004
Dicrotendipes	nervosus	(Staeger)				25	25	2		2	2	6	31	0.142
Dicrotendipes	notatus	(Meigen)				55	55						55	0.252
Endochironomus	albipennis	(Meigen)				92	92				23	23	115	0.528
Endochironomus	tendens	(Fabricius)									1	1	1	0.004
Glyptotendipes	pallens	(Meigen)				450	450				24	24	474	2.177
Glyptotendipes	paripes	(Edwards)				111	111						111	0.509
Harnischia	fuscinans	Kieffer	1	6	15	7	29		2	3		5	34	0.156
Kiefferulus	tendipediformis	Goetghebuer				196	196						196	0.900
Lipiniella	arsenicola	Shilova			2		2						2	0.009
Microchironomus	tener	(Kieffer)		4	3		7			1		1	8	0.036
Microtendipes	chloris	(Meigen)				1	1						1	0.004
Parachironomus	arcuatus	(Goetghebuer)		1		220	221	3			9	12	233	1.070
Parachironomus	camptolabis	(Kieffer)		1			1						1	0.004
Paralauterborniella	nigrohalteralis	(Malloch)		15	37	1	53		1			1	54	0.248
Paratendipes	albimanus	(Meigen)	1	7	302	17	327		13	6		19	346	1.589
Phaenopsectra	flavipes	(Meigen)		1		16	17	3	2	2	1	8	25	0.114
Polypedilum	albicorne	(Meigen)		1			1						1	0.004
Polypedilum	convictum	(Walker)		4		19	23						23	0.105
Polypedilum	cultellatum	(Goetghebuer)		1	10	3	14	1	4			5	19	0.087
Polypedilum	laetum	(Meigen)		1	1		2						2	0.009
Polypedilum	nubeculosum	(Meigen)		3	5	75	83	10	34	47	6	97	180	0.826
Polypedilum	pedestre	(Meigen)			1		1						1	0.004
Polypedilum	pullum	(Zetterstedt)		25	82	29	136	6	40	8		54	190	0.872
Polypedilum	quadriguttatum	Kieffer	4	31	86	2	123						123	0.565
Polypedilum	sordens	Van der Wulp				64	64	1	1		2	4	68	0.312
Stictochironomus	maculipennis	(Meigen)			7		7			3		3	10	0.045
CHIRONOMINAE Tanytarsini														
Cladotanytarsus	manicus	(Walker)	2	26	99	33	160	3	3	15		21	181	0.831
Cladotanytarsus	vanderwulpi	(Edwards)			3		3						3	0.013
Micropectra	atrofasciata	Kieffer	20	24	36	8	88	39	24			63	151	0.693
Neozavrelia	fuldensis	Fittkau	3	1	1		5	1				1	6	0.027
Paratanytarsus	dissimilis	Johannsen	1	12	65	568	646	85	20	52	55	212	858	3.941
Paratanytarsus	inopertus	(Walker)	1		15	205	221	47	1	10	13	71	291	1.341
Paratanytarsus	penicillatus	(Goetghebuer)				1	1						1	0.004
Paratanytarsus	tenellus	(Goetghebuer)				82	82						82	0.376
Rheotanytarsus	pentapoda	Kieffer							4			4	4	0.018
Rheotanytarsus	rhennanus	Klink	69	55	49	3	176	16	2			18	194	0.891
Stempellina	almi	Brundin	1		1		2						2	0.009
Stempellina	subglabripennis	Brundin		1			1						1	0.004
Tanytarsus	brundini	Lindeberg		1	3	16	20		1			1	21	0.096
Tanytarsus	buchonius	Reiss & Fittkau				1	1				4	4	5	0.022
Tanytarsus	curticornis	Kieffer		1	2		3						3	0.013
Tanytarsus	ejuncidus	(Walker)		1	19	1	21	13	10	18	1	42	63	0.289
Tanytarsus	eminulus	(Walker)		9	56	222	287	28	21	17		66	353	1.621
Tanytarsus	henzensis	Goetghebuer		1	3	9	13		1	3		4	17	0.078
Tanytarsus	mendax	Kieffer			9		9						9	0.041
Tanytarsus	sigriticollis	Goetghebuer			1		1						1	0.004
Tanytarsus	pallidicornis	Walker				9	9			1	1	2	11	0.050
Tanytarsus	recurvatus	Brandla								1		1	1	0.004
Virgatanytarsus	Pel	Langton 91	1		3	1	5			5		5	10	0.045
Total number of specimens			6 013	3 175	4 946	3 613	17 747	1 517	1 265	915	322	4 019	21 766	
Species richness			64	70	83	84	130	43	50	37	27	72	137	

from northern and western Europe ; *T. nigricollis* is known from Belgium and Germany.

Table 2 gives for each new species, the information on their biology and ecology : emergence period, habitat, substrata colonised (pupae), current velocity and water temperature at sampling dates. The last column presents the information provided by Langton (1991, 1995) on known habitats of each species. It is interesting to note that :

- 8 of the 12 newly recorded species are exclusively collected in the floodplain waters in the temporarily connected side arm (SA₂) and oxbow (Ox), corresponding with the usual lentic sites they colonise : lakes, ponds, ditches or other lentic systems;

- 4 new recorded species were collected in February, which underlines the usefulness of winter collections in spite of the sampling difficulties met in this period;

- 8 of the 12 new recorded taxa were exclusively collected by drift, which highlights the effectiveness of this method for faunal and biogeographic studies.

3.2. Contribution of the floodplain waters

3.2.1. Biodiversity in the four studied sites

With 88 species identified in the 3 935 specimens collected, the oxbow appears the most diverse sampling site : $R/\log E = 24.5$ species (Fig. 4a). Moreover, we note the increase of specific richness related to the lentic status of the sites, whether the site be permanently (Ox) or temporarily (SA₂) disconnected (Fig. 4a).

The high intrinsic species richness brought by floodplain waters is confirmed by their high number of site specific species (Fig. 4b). Respectively 13 and 21 species were collected exclusively in the temporarily

connected side arm (SA₂) and in the oxbow (Ox), whereas only 7 to 9 site specific species were exclusive to the two lotic sites (SA₁ and MC).

3.2.2. Faunal interaction between the main channel and floodplain waters

It is well-known that the Chironominae sub-family dominates the chironomid community in the potamal zones. In the potamal 6th order section of the Garonne river this point is confirmed as shown by the ratio Orthocladiinae/Chironominae calculated on the total population ($Or/Ch = 0.74$). A site-differentiated calculation of the ratio reveals that this trend is true in the floodplain waters but is reversed in the main channel where the sub-family Orthocladiinae dominates ($Or/Ch = 1.2$) (Table 3).

Nevertheless, half of Orthocladiinae (51 % in our case study) found in the potamal zone are potamobiont species, living in fast to slow flowing warm waters and lakes. Each species was coded according to the habitat data found in the literature in three categories :

- 1) rheophilous (R : species living usually in streams, rivers, drains and all kinds of fast flowing waters) ;

- 2) dual (species living equally in running and standing waters) ;

- 3) limnophilous (L : species living in all kinds of standing waters like lakes, ponds, ditches, pools, gravel pits, bogs, peat pools, submerged meadows...).

Overall, the chironomid community is dominated by limnophilous species ($R/L = 0.85$) (Table 3).

Considering each site separately, 14 to 17 limnophilous species were collected only in the main channel

Table 2. Ecological information on the 12 new recorded taxa in the Garonne.

Tableau 2. Informations sur l'écologie des 12 nouveaux taxa recensés sur la Garonne.

	Sampling period	Sampling site	Sampling method	Substrata	Current velocity (cm.s ⁻¹)	Temperature (°C)	Langton (1991-1995) observations
<i>Corynoneurella pahudosa</i>	May to October	MC SA ₁ SA ₂	Drift net		0 to 5	15.6 to 25	
<i>Eukiefferiella</i> Pe2	February	SA ₁	Surber net	Macrophytes	0 to 5	8.9	Stream
<i>Limnophyes pahudis</i>	February	Ox	Drift net		0 to 5	10.4	Larvae on leaves in ditches
<i>Parakiefferiella scandica</i>	March	SA ₂	Drift net		0 to 5	13.6	Northern lakes
<i>Thienemannella</i> Pe2a	May to November	SA ₁ SA ₂	Drift & Surber net	Macrophytes	0 to 5	16.1	Stream
<i>Thienemannella</i> Pe2b	September to May	MC SA ₁ SA ₂	Drift net		0 to 5	6 to 18	Stream
<i>Chironomus rithmakiensis</i>	November & February	Ox	Drift net		0 to 5	10.4 to 14.6	Pools, Finland
<i>Cryptochironomus obreptans</i>	June to October	SA ₂ Ox	Drift net		0 to 5	14.3 to 28.3	Drains & shallow lakes
<i>Paratanytarsus penicillatus</i>	February	Ox	Drift net		0 to 5	10.4	Lakes & bogs
<i>Tanytarsus buchoni</i>	February	Ox	Drift & Surber net	Muddy gravel & roots	0 to 5	10.4	Peat pools & boggy seepages
<i>Tanytarsus nigricollis</i>	September	SA ₂	Drift net		0 to 5	17.1 to 18.8	Lakes
<i>Tanytarsus recurvatus</i>	September	SA ₂	Surber net	Muddy gravel & boulders	0 to 5	16.5 to 27.5	Northern & montane lakes

Fig. 4. Compared biodiversity. a) Compared relative species richness. R : species richness, E : number of specimens ; b) Compared site specific species number. N : number of species exclusively found in the sampling site considered, E : number of specimens. MC : Main channel, SA₁ : Upstream side arm, SA₂ : Downstream side arm, Ox : Oxbow.

Fig. 4. Biodiversité comparée. a) Richesse spécifique relative comparée des 4 sites d'échantillonnage. R : Richesse spécifique, E : effectif ; b) Nombre d'espèces spécifiques comparé entre les 4 sites d'échantillonnage. N : nombre d'espèces recensées uniquement dans le site considéré, E : effectif. MC : Chenal principal, SA₁ : Bras secondaire amont, SA₂ : Bras secondaire aval, Ox : Bras mort.

(MC) and in the permanently connected side arm (SA₁) whereas 24 to 40 were recorded only in the temporarily connected side arm (SA₂) and in the oxbow (Ox). The Rheophilous/Limnophilous ratio decreases along a positive gradient of lentic conditions from 2.50 (MC) to 0.48 (Ox).

Considering limnophilous species common to the three floodplain sites (SA₁, SA₂, Ox) and to the main channel (MC), 9 to 12 of the 14 limnophilous species collected in the main channel come from the lentic

zones (Table 4). The number of site-specific limnophilous species corresponds with a positive gradient of lentic conditions too.

4. Discussion

The high species diversity provided by the floodplain backwaters has been underlined by several authors (Décamps 1996, Ward 1998) ; for macroinvertebrates (Elstadt 1986, Hornbach et al. 1993), and other

Table 3. Between-sampling site comparison of the structure of the chironomid population according to the susceptibility of the species to the flood. Number of species and ratio. MC : Main channel, SA₁ : Upstream side arm, SA₂ : Downstream side arm, Ox : Oxbow ; Or : Orthocladiinae ; Ch : Chironominae.

Tableau 3. Comparaison inter-site de la structure des populations considérant l'affinité des espèces pour le courant. Nombre d'espèces et ratio. MC : Chenal principal, SA₁ : Bras secondaire amont, SA₂ : Bras secondaire aval, Ox : Bras mort ; Or : Orthocladiinae ; Ch : Chironominae.

	MC	SA ₁	SA ₂	Ox	Total
Or/Ch	1.2	0.8	0.8	0.8	0.74
Rheophilous	35	35	30	19	46
Dual	32	31	37	28	39
Limnophilous	14	17	24	40	54
Ratio R/L	2.5	2.1	1.2	0.5	0.85

faunal groups such as microcrustaceans (Amoros & Chessel 1985) and fishes (Bain & Boltz 1989). Remembering that wetlands have been considered to be the most diverse habitats since the International Convention of Ramsar in 1971, these studies justify that, at the scale of the floodplain, backwaters can be considered true wetlands (Bayley 1995).

The results for the River Garonne agree with the previous studies. In fact, the faunal diversity of floodplain waters is characterised by two overlapping components : high number of species and high number of site specific species. More than any other, this last point reveals the real faunal singularity of backwaters in comparison with fast flowing sites. Strictly, the main channels of the potamal sections, with both fast flowing and standing water habitats, should support the maximum species diversity due to their obvious hydro-morphological heterogeneity. This is not so and it is justifiable to think that backwaters are the main support of global diversity in the potamal sections of rivers. This could explain why, in recent European studies (Franquet 1996, Balzer 1997, Garcia & Laville 2000), the potamon is surprisingly given as the most diverse, whereas it was commonly accepted that the greatest specific richness was found in the rhithral sections of rivers (Minshall et al. 1985).

Additionally, in the backwaters of the Garonne river, the two components of faunal diversity relate to their degree of connectivity with the main channel, the mo-

Table 4. Number and percentage of common limnophilous species between sampling sites. In bold : number of limnophilous species exclusively found in the site considered. MC : Main channel, SA₁ : Upstream side arm, SA₂ : Downstream side arm, Ox : Oxbow.

Tableau 4. Nombre et pourcentage d'espèces limnophiles communes aux différents sites prospectés. En gras : nombre d'espèces limnophiles trouvées exclusivement dans le site considéré MC : Chenal principal, SA₁ : Bras secondaire amont, SA₂ : Bras secondaire aval, Ox : Bras mort.

		MC	SA ₁	SA ₂	Ox
		%			
MC	Species nb.	1	71	64	86
SA ₁		10	2	59	71
SA ₂		9	10	7	63
Ox		12	12	15	21

re disconnected site generating the highest species richness. This result does not agree entirely with macroinvertebrate diversity patterns described in the Rhine and Danube floodplains. If the highest species richness is always found in backwaters (Bis & Palm 1990, Tockner & Bretschko 1996), it is also, for the most part, positively correlated with the highest degree of connectivity (Gepp et al. 1985, Tockner et al. 1999). For example, Obrdlik & Fuchs (1991) collected 19 species of gastropods in the stable backwaters versus 30 species in the regularly flooded ones. In the same way, Tockner & Bretschko (1996) observed the maximum macroinvertebrate diversity in plesiopotamal waterbodies, a geomorphological type defined as connected to the main channel 43 to 160 days per annum. Nevertheless, the complex and varied nature of diversity patterns across connectivity gradients (Ward et al. 1999, Tockner et al. 2000) as well as their dependence on hydro-geomorphological characteristics of each river must be borne in mind (Garcia 2000). A recent study by Tockner et al. (1999) on species diversity patterns across hydrological connectivity gradients in the Danube floodplain system, based on four groups of living organisms - macrophytes, molluscs, odonates and amphibians - additionally highlights various responses obtained according to the group considered.

The studied section of the river Garonne has both riffles and lowland pools in the main channel and floodplain waters. In term of typology it corresponds to a transition section defined as a mixed epipotamal-

metapotamal section, between the rhithral - upper part, upstream of Toulouse - composed mainly of riffles, and the hypopotamal - lower part, downstream of the confluence with the Tarn tributary - a slow flowing water dominated part.

If the studied section is a real potamon as shown by the characteristic prevalence of the Chironominae sub-family in the whole community (Lehmann 1971), the described constitutional duality results in a strong spatial segregation between limnophilous and rheophilous populations. This status is generated and maintained by the embankment of the main channel since 1958. By increasing the current velocities and limiting the formation of riparian lentic zones, the embankment strengthens the epipotamal nature of the main channel with riffles at the expense of its metapotamal nature of lowland pools and riverside lentic zones. Additionally, the natural fluctuation of discharge associated with the functioning of numerous water-plants is responsible for a strong daily variation in the water level which can be 60 % of the mean daily discharge (Danneville 1995).

Overall, this explains why the previous investigation prospecting of this same section of the main channel, based on drift samples, provided a population dominated by the Orthoclaadiinae.

It follows that the conservation of floodplain waters is required to preserve limnophilous populations. Moreover, to maintain the limnophilous populations it is essential that colonisation of lentic zones in the main channel can occur, whether these lentic zones are permanent or sporadically generated by seasonal hydrodynamics. This point has already been underlined by Amoros & Roux (1988) as many studies have shown the drift of organisms from backwaters into the main stream. This phenomenon has been demonstrated for the juveniles of fishes but also for macroinvertebrates of the Upper Mississippi river (Eckblad et al. 1984, Sheaffer & Nickum 1986b) and for those of the Rhône river (Cellot & Bournaud 1986, 1988). Nevertheless, chironomid colonisation of the lentic zones of the main channel is favoured also by laying imagoes of limnophilous species living close to the main channel. Consequently, the nearness of the backwaters also governs the species richness of the lentic zones of the main channel, as shown by the high number of limnophilous species common to the main channel and floodplain sites.

Considering that all kinds of fragmentation of ecosystems reduces their biodiversity, the studied section of the River Garonne appears to be a threatened ecosystem which owes its species richness mainly to the

persistence of the remnant more or less isolated floodplain backwaters.

Overall, as already revealed by the faunal inventory of the potamal zone of the sandy Loire river (Garcia & Laville 2000), this study highlights the topicality and value in investigating potamal regions of large European rivers in order to increase knowledge of chironomid biodiversity, ecology and biogeography.

The regulation of rivers and their disturbance by human activities started at the beginning of the last century (Walker 1985, Ward & Stanford 1986, Fruget 1992), underlining the urgency for investigating the less disturbed of them, as many of the original species have been already lost without knowing what their ecological role was (Davies & Walker 1986).

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