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Continuous drift samples of macroinvertebrates in a large river, the Danube in Austria

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SUMMARY. 1. A new method is described for sampling the drift in large rivers continuously and automatically, using equipment based on the marine, continuous plankton sampler of Hardy (1936).

2. Between April and November 1989, about 790 h were sampled continuously, equivalent to a water volume of 2937 m^3 and the total catch was 527 drifting macroinvertebrates, in forty-nine taxa. Twenty-five of these taxa are recorded in the drift for the first time and twenty-eight of the drifting taxa were present in benthos samples from the Danube.

3. Total drift density varied between 12 and 31 animals per 100 m^3 of water sampled throughout the year, with a maximum of 31 animals in May. The composition of major faunal groups showed a significant seasonal pattern, with Oligochaeta and Diptera predominant in spring, Crustacea and Insecta in summer and only Crustacea in autumn. The overall density of the macrozoobenthos from October 1986 to December 1987 was about 19 360 animals m^{-2} and the proportion of total benthos animals, drifting at any instant in time, ranged from 0.0026 to 0.0064%.

4. The relationship between drift density day^{-1} and mean daily discharge was described by a power-function. Total mean drift rate of macroinvertebrates in the Danube was estimated to be 13 600 000 animals per 24 h and the mean drift distance was estimated to vary between about 4 and 31 m, dependent on the animal group and the water velocity.

5. No obvious consistent diel pattern could be established from the continuous samples, and no marked diel rhythm could be detected for Oligochaeta, Diptera larvae and Crustacea.

Introduction

The term 'invertebrate drift' describes the downstream movement in the water column of benthic invertebrates that usually live on or amongst the substratum of streams and rivers. Although there are a few earlier records (e.g. Needham, 1928; Mottram, 1932; and references in Elliott, 1967), most information on invertebrate drift has appeared in the last 25 years. This early work stimulated many investigations on the mechanisms responsible for invertebrate drift, on the role of drift as a dispersal mechanism

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and on the importance of drift as a food for fish, especially salmonids. There are now over 400 publications in this field and several excellent reviews (Waters, 1972; Bournaud & Thibault, 1973; Müller, 1974, 1982; Adamus & Gaufin, 1976; Williams, 1981; Wiley & Kohler, 1984; Statzner, Dejoux & Elouard, 1984; Brittain & Eikeland, 1988). Despite this vast information on drift, knowledge about this phenomenon in large rivers is scarce, notable exceptions being the Volga, the Amur, the Mississippi, the Missouri, and the upper Rhône (summarized by Cellot, 1989). One reason for this lack of information is that most methods for measuring drift are easy to use only in streams or small rivers (summarized by Elliott, 1970). As most drift records result from sampling periods of a few minutes or several hours, there is a lack of information on continuous measurements of the drift.

Through the ecosystem study at Altenwörth, 'Impacts of a Hydro-Power Plant on the Danube' (Grosina, 1985; Hary & Nachtnebel, 1989), sponsored by the Austrian Man and Biosphere Programme (MaB 5/9 and 20), it was possible to finance the construction of a continuous drift sampler, similar to the marine sampler of Hardy (1936) and to use this apparatus to measure drift continuously in a large river for the first time.

The purpose of the present study was to analyse the composition of the macroinvertebrate drift in a large river, the Austrian Danube, to obtain some information on the mobility of the macrozoobenthos by relating the number of animals in the water column to the density of animals on the bottom, to describe the pattern of drifting animals when sampled continuously and finally to present a rough estimate of distances travelled by the animals, using the formula given

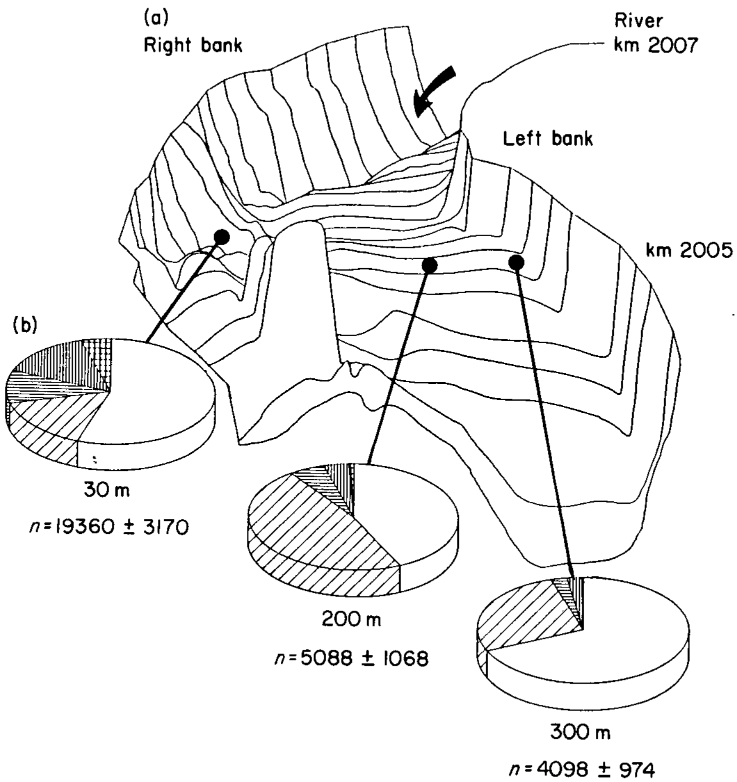

FIG. 1. Sampling sites 30, 200 and 300 m from the right bank at river kilometre 2005 (from the river mouth); (a) morphology of the river bed seen from downstream; (b) relative abundance of the major groups of macroinvertebrates: *n*, mean number of macroinvertebrates m^{-2}±SE; □, Oligochaeta; ▨, Diptera; ▥, Trichoptera; ▤, Crustacea; ■, Mollusca. The arrow indicates the flow direction.

TABLE 1. Summary of information on hydrological and grain size variables, characterizing three sites (30, 200 and 300 m from the right bank) at river kilometre 2005 (from the river mouth) at different levels of discharge. V = water velocity (max = maximum, aM = arithmetic mean, 50 cm = 50 cm above the bottom); $Q_{1\phi}$, Md_{ϕ}, $Q_{3\phi}$ = first, second and third quartile of grain size distribution

Total discharge ($m^3 s^{-1}$)	677			1836			3115		
Date	11 Dec 1986			24 Aug 1987			22 Apr 1987		
Distance from right bank (m)	30	200	300	30	200	300	30	200	300
Water depth (m)	2.5	2.9	2.8	3.5	3.5	3.0	4.2	4.7	5.0
V_{max} ($m s^{-1}$)	0.7	0.9	0.9	1.3	1.7	1.5	1.6	2.3	2.1
V_{aM} ($m s^{-1}$)	0.5	0.8	0.7	1.1	1.5	1.3	1.3	1.9	1.7
V_{50cm} ($m s^{-1}$)	0.4	0.5	0.5	0.7	1.0	0.9	0.9	1.0	1.1
$Q_{1\phi}$ (mm)	31.3	12.0	8.9	29.8	15.2	8.0	26.3	15.3	9.7
Md_{ϕ} (mm)	46.3	16.7	16.4	42.6	17.0	12.9	33.8	17.4	15.9
$Q_{3\phi}$ (mm)	61.1	20.2	20.1	55.8	19.4	19.2	70.1	21.3	19.0
River bed movement	No	No	No	No	Yes	No	No	Yes	Yes

by Elliott (1971a). The latter allows some speculations on the colonization of animals near the barrage. The present investigation is the first study quantifying the drift of macroinvertebrates in the Danube.

Study area and sampling sites

The study area is situated 25 km upstream of the dam of the river impoundment Altenwörth (river kilometre 1980.4; 48° 23′ N; 15° 51′ E; altitude 186 m). The sampling site is situated at the beginning of the backwater zone of the impounded river. At river kilometre 2005 the Danube is about 330 m wide, with a depth varying across the river from 3.0 to 3.5 m at a mean discharge of 1836 $m^3 s^{-1}$ (Fig. 1a, Table 1). The total discharge fluctuates between 592 and 8240 $m^3 s^{-1}$, based on data between the period 1976 and 1989, with low values in late autumn and high values mainly in late spring or early summer. As the mean annual water temperature is 9.5°C and temperature ranges from 0 to 20°C, this part of the river is characterized as 'summercool' (Pleskot, 1951). As the study area is described in detail in Humpesch & Elliott (1990), only a brief account is given here (summarized in Table 1). At mean discharge, water velocity ranges from a V_{max} of 1.3 $m s^{-1}$ near the right bank to that of 1.7 and 1.5 $m s^{-1}$ in the mid-channel and near the left bank, respectively. Further changes in the velocity occur at different levels of discharge. There is a permanent gradient of grain size across the river, ranging from a $Q_{3\phi}$ of 55.8 mm near the right bank to that of 19.2 mm near the left bank. Due to the different grain sizes in the cross-section, the stability, and therefore the mobility, of the river-bed sediment varies. Along this particle-size gradient across the river, there is an obvious change in the structure of the fauna. Four groups of macroinvertebrates, Oligochaeta, Diptera, Crustacea and Trichoptera, are dominant near the right bank, whereas in mid-channel and near the left bank only two groups, Oligochaeta and Diptera, are dominant (Fig. 1b).

In the present study, drift was investigated only at the site 30 m from the right bank. As there were cross-sectional differences in the density and composition of the fauna across the river, caution is necessary in applying the drift results from this site to the whole cross-section of the river.

Methods

Design of the drift sampler and its application in the field

Based on the marine, continuous plankton sampler (Hardy, 1936), a continuous drift sampler was constructed by R. Niederreiter (Fig. 2a). The sampler is 1.7 m long and has a width and height of about 0.5 m. The total weight is 80 kg. Sampling in the field requires a high- powered

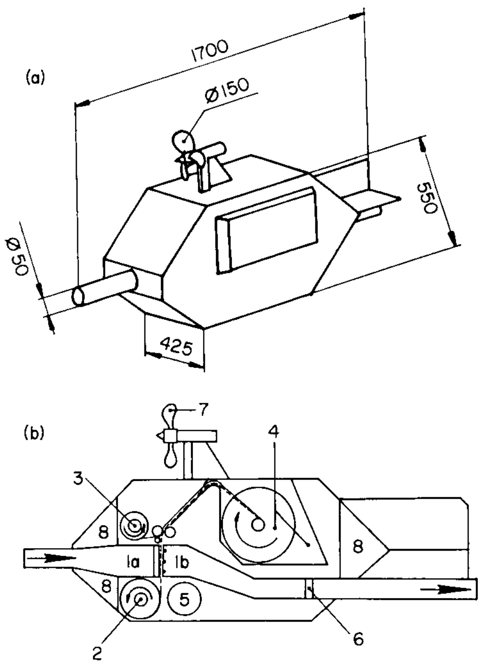

FIG. 2. Continuous drift sampler (after Hardy, 1936; modified by R. Niederreiter). (a) External view of the sampler (units in mm). (b) Cross-section: 1a = water tunnel (the arrow indicates the flow direction); 1b = sampling gap; 2 = spool containing gauze band; 3 = spool containing polyethylene foil; 4 = preservation tank filled with formaldehyde (with storage spool); 5 = time recorder; 6 = water meter; 7 = propeller; 8 = buoyancy volume.

motor boat for exposure of the apparatus and a buoy to which the sampler can be fixed by means of a long rope. Because of its buoyancy, the sampler floats on the surface of the water and can be lowered to the desired depth by an anchoring weight and its rope. In this study the sampler was lowered to two positions, 0.5 m above the river bottom and 0.5 m below the water surface.

General performance

The following sampling procedure was used (Fig. 2b). The gauze band (2), mesh size 400 μm, is steadily drawn through the water tunnel (1a), acting as a sieve that filters drifting organisms. After the sampling gap (1b) has been passed, the gauze band is covered by polyethylene foil (3) and both tapes are stored in the preservation tank (4), which contains formaldehyde solution. The polyethylene foil prevents trapped animals from being swept away from the gauze band after having passed the current-exposed sampling gap, and also separates single gauze band layers on the storage spool (4). The whole device is driven by a propeller (7), using the water current as an energy supply. Therefore, the speed of the gauze band is proportional to the water velocity. The duration of a continuous sampling session is restricted to the total length of the gauze band, and the latter determines the whole dimensions of the sampler. In the present study, the sampler allowed a continuous sampling period of almost 14 days.

The gauze band is marked equidistantly, at 50-cm intervals and the time recorder (5) notes the time required for the gauze band to pass the sampling gap from one mark to the next. Thus, the marks can be related to a definite time interval and the samples can be timed. The total volume of water sampled is measured by a water meter (6). Sampling units were obtained by washing out the gauze band, section by section, in the laboratory. The material was sorted into different groups of macroinvertebrates, larval and pupal exuviae of aquatic insects and planktonic Crustacea, but only the macroinvertebrates (>400 μm) were included in the present study.

Timing of the samples

As the gauze band was marked every 50 cm and the timing of the marks was recorded, it was possible to estimate the total length of band used in a given period between 2 and 6 h. The 4-h period was chosen because this interval showed best the temporal pattern. The same intervals were used for all sampling sessions to make the results comparable. The actual speed of the band and therefore the length used in a sampling session was of course related to the water velocity through the sampler. As both the timed samples and the fixed 4-h interval did not overlap for all samples, the following timing procedure was chosen: the whole timed sample was included in a fixed 4-h interval, if its time overlapped for half or more than half of the time of the fixed 4-h interval.

Data analysis

A chi-squared contingency table (Elliott, 1977) was used to test differences in the drift composition of the major taxa between single sampling sessions. The differences between the drift numbers 0.5 m above the bottom and 0.5 m below the surface and the differences between the day and the night drift were tested with a Mann–Whitney *U*-test.

The proportion of benthos in the drift (P, %) at any instant in time was calculated by the formula

$$P = \frac{xD \times 100}{X - xD} \quad (1)$$

where x is the number of drifting individuals per m^3, X is the number of benthos individuals (m^{-2}) and D is the average water depth (m) (Elliott, 1967).

Results

Fauna in the drift

A comparison between the forty-nine taxa present in the drift (Table 2) and the taxa recorded in the bottom samples from the previous year at this site (see Appendix) showed that the Lamellibranchiata, Polychaeta and Hirudinea were absent from the drift samples, and that twenty-one taxa were recorded in the drift samples, but not in the benthos samples of the previous year.

Seasonal fluctuations in numbers in the bottom drift

In the sampling period between April and November 1989, which is equivalent to 794.3 h of continuous sampling and a water volume of 2937.6 m^3, 527 macroinvertebrate individuals were found. The total number fluctuated seasonally, with high values in May and low values in November (Table 3a). Drift densities were similar in each session, ranging from twelve to eighteen individuals per 100 m^3, the exception being the sampling session in May with 31 individuals per 100 m^3. Therefore, apart from the sample in May, the number of macroinvertebrates per standard water volume did not fluctuate a great deal throughout the year, even though the discharge ranged from 1100 to 2873 $m^3 s^{-1}$. The higher density of animals in May did not coincide with high levels of discharge (Table 3b). In contrast, the composition of the major faunal groups changed significantly throughout the year ($P<0.001$). Oligochaeta and Diptera larvae were predominant in spring, Crustacea and Insecta larvae in summer and only Crustacea in autumn. Such a seasonal pattern could not be detected for groups represented by very low numbers (Table 3b).

On one occasion in May 1989, a comparison was undertaken between the drift density 0.5 m above the bottom and 0.5 m below the surface. The two densities were just significantly different ($P<0.05$), with 31.3 animals per 100 m^3 near the bottom and 23.2 near the surface.

The drift rate calculated from the original data seems to show a strong seasonal pattern, with high values in May and low values in November (Table 3c). When relating these results to the actual discharge, a power function fitted the data ($\log N_d = \log a + b \log Q$, where N_d = numbers per day, Q = mean daily discharge, constant $\log a = -9.27$, constant $b = 3.15$, $P<0.001$, $r^2 = 0.51$). As these actual numbers result from periods with different portions of the total discharge sampled, ranging from 2.6×10^{-5} to 8.4×10^{-5}%, the actual numbers were calibrated to a standard proportion of 10^{-4}% of the total discharge. This conversion equalizes the pattern, but the high value in May remains (Table 3c). The power function is still applicable, but the coefficient of determination decreases from $r^2 = 0.51$ to $r^2 = 0.21$ ($\log a = -4.05$, $b = 1.65$, $P<0.01$).

Relationship between drift and benthos

The estimated number of individuals drifting in the water column over a m^2 at any instant in time ranged from 0.0026 to 0.0064% of the overall density (19 360±3170 individuals m^{-2}) of the macrozoobenthos (Table 3d).

Diel variations of drift

The total number of animals taken per 24 h varied within and between the sampling periods (Table 3c), but the day and night drift rates were not significantly different ($P>0.05$) throughout the year. When the daily numbers were analysed in their temporal succession through the continuous samples, no obvious consistent pattern could be established (Fig. 3). The patterns as a whole do not seem to be influenced markedly by the discharge, e.g. the diel pattern in June did not follow the increase and that in November did not follow the decrease in discharge (Fig. 3).

TABLE 2. Taxa of benthic macroinvertebrates occurring in the drift, showing which of the latter occurred in the benthos samples from the Danube between October 1986 and December 1987 and in previous European drift studies (nomenclature after Illies, 1978)

	Taxa occurring		
	in the drift of the Danube	in the benthos of the Danube	in the drift in previous studies
Coelenterata			
Hydrozoa	*Hydra* sp.	no	yes
Plathelminthes			
	Tricladida	yes	yes
Mollusca			
Gastropoda	*Ancylus fluviatilis* Müller	yes	yes
	Potamopyrgus jenkinsi (Smith)	yes	yes
	Valvata sp. cf. *piscinalis* Müller	no	yes
Annelida			
Oligochaeta	*Chaetogaster diastrophus* (Gruithausen)	yes	yes
	Nais barbata (Müller)	no	no
	N. bretscheri Michaelsen	yes	no
	N. elinquis Müller	yes	yes
	Tubificidae	yes	yes
Arachnida			
Acari	*Sperchonopsis verrucosa* (Protz)	no	no
Crustacea			
Isopoda	*Jaera istri* Veville	yes	no
Amphipoda	*Chaetogammarus tenellus* Sowinskyi	yes	no
	Dikerogammarus haemobaphes fluviatilis Martinov	yes	yes
	Corophium curvispinum Sars	yes	yes
Insecta			
Ephemeroptera	*Baetis* spp.	yes	yes
	Caenis luctuosa (Burmeister)	no	yes
	C. rivulorum Eaton	no	yes
	Heptagenia sp.	yes	yes
Plecoptera	Nemouridae	no	yes
	Leuctra sp.	no	yes
Coleoptera	*Elmis* sp.	yes	yes
Trichoptera	*Brachycentrus subnubilus* Curtis	yes	yes
	Hydropsyche bulgaromanorum Malicky	no	no
	H. contubernalis McLachlan	no	yes
	Lepidostoma hirtum Fabricius	yes	yes
	Hydroptila sp.	no	yes
	Oligoplectrum maculatum Fourcroy	yes	no
	Psychomyia pusilla Fabricius	yes	yes
	Rhyacophila sp.	no	yes
	Tinodes sp.	no	no
Diptera	*Brillia longifurca* Kieffer	yes	no
	Cricotopus bicinctus (Meigen)	yes	no
	Eukiefferiella gracei (Edwards)	yes	no
	E. lobifera Goetghebuer	yes	no
	E. minor (Edwards)	no	no
	Micropsectra atrofasciata-agg. Kieffer	no	no
	Odontomesa fulva (Kieffer)	no	no
	Orthocladius (Euorthocladius) rivicola (Kieffer)	yes	no
	O. sp.cf. *excavatus* (Brundin)	yes	no
	O. s.str. *saxicola* (Kieffer)	yes	no
	O. (Eu.) thienemanni (Kieffer)	yes	no
	Paratanytarsus sp.cf.*inopertus* (Walker)	no	no
	Paratrichocladius rufiventris (Meigen)	yes	no
	Polypedilum convictum (Walker)	no	no
	Rheotanytarsus sp.cf.*muscicola* Kieffer	no	no
	Thienemannimyia sp.cf.*laeta* (Meigen)	no	no
	Simulium galeratum Edwards	yes	no
	Antocha sp.	no	yes

TABLE 3. Seasonal variation of macroinvertebrates in the drift, 30 m from the right bank (river kilometre 2005); showing the dates of the sampling periods, the mean discharge (with range) during the sampling periods ($m^3 s^{-1}$), the time (h) continuously sampled and the water volume filtered (m^3). (a) Total number of individuals; (b) drift densities: given as total numbers (*n*) per 100 m^3 for each group and as percentage of the total number (the category 'Others' includes groups which were seldom found) for all animals in each sampling session and overall; (c) drift rates: given as arithmetic mean (with range) numbers sampled per day for original proportion of discharge sampled and calibrated for a standard proportion of 10^{-4}% of the total discharge; (d) proportion of macroinvertebrates in the water column above 1 m^2 given as percentage of the arithmetic mean number (with standard error) of the bottom fauna from December 1986 to December 1987 (19360±3170 individuals m^{-2}; H. Petto, pers. comm.)

Period (1989)	Apr(20–26)		May(2–8)		Jun(22–27)		Aug(11–16)		Nov(10–21)		Total
Mean discharge $m^3 s^{-1}$	1921		1947		2437		2072		1434		1962
(with range)	(1776–2146)		(1838–2236)		(2211–2873)		(1854–2310)		(1100–2074)		(1100–2873)
Sampling time (h)	144.3		143.5		121.3		121.9		263.3		794.3
Volume sampled (m^3)	638.3		542.4		660.6		742.4		353.9		2937.6
(a) Individuals sampled	81		170		120		93		63		527
(b) Drift densities	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	%
Oligochaeta	6.7	53.1	15.7	50.0	3.0	16.7	0.7	5.4	0.9	4.8	29.1
Mollusca	0.3	2.4	0.2	0.6	0.3	1.7	0.1	1.0	0.3	1.6	1.3
Crustacea	1.4	11.1	1.8	5.9	8.2	45.0	7.5	60.2	15.3	85.7	37.0
Ephemeroptera (larvae)	0.2	1.3	0.6	1.8	0.5	2.5	0	0	0.3	1.6	1.6
Trichoptera (larvae)	0.3	2.4	1.5	4.7	3.2	17.5	2.0	16.1	0	0	7.5
Diptera (larvae)	3.5	27.2	11.4	36.5	3.0	16.7	1.9	15.1	0.6	3.2	22.0
Others	0.3	2.4	0.2	0.6	0	0	0.3	2.2	0.6	3.2	1.4
Total	12.7	100	31.3	100	18.2	100	12.5	100	17.8	100	100
(c) Percentage of total discharge sampled (%)	6.4×10^{-5}		5.4×10^{-5}		6.2×10^{-5}		8.4×10^{-5}		2.6×10^{-5}		
Drift rate (nos·day^{-1}) mean (range) sampled	13.5 (7–20)		28.3 (5–60)		24.0 (14–30)		18.6 (6–50)		5.7 (1–13)		
Standardized drift rate (nos·day^{-1}) for 10^{-4}% of total discharge mean (range) calibrated	21.1 (11–31)		52.5 (9–111)		38.7 (23–48)		22.1 (7–60)		22.0 (4–50)		
(d) Proportion of benthos in drift (%)	0.0026		0.0064		0.0041		0.0026		0.0033		

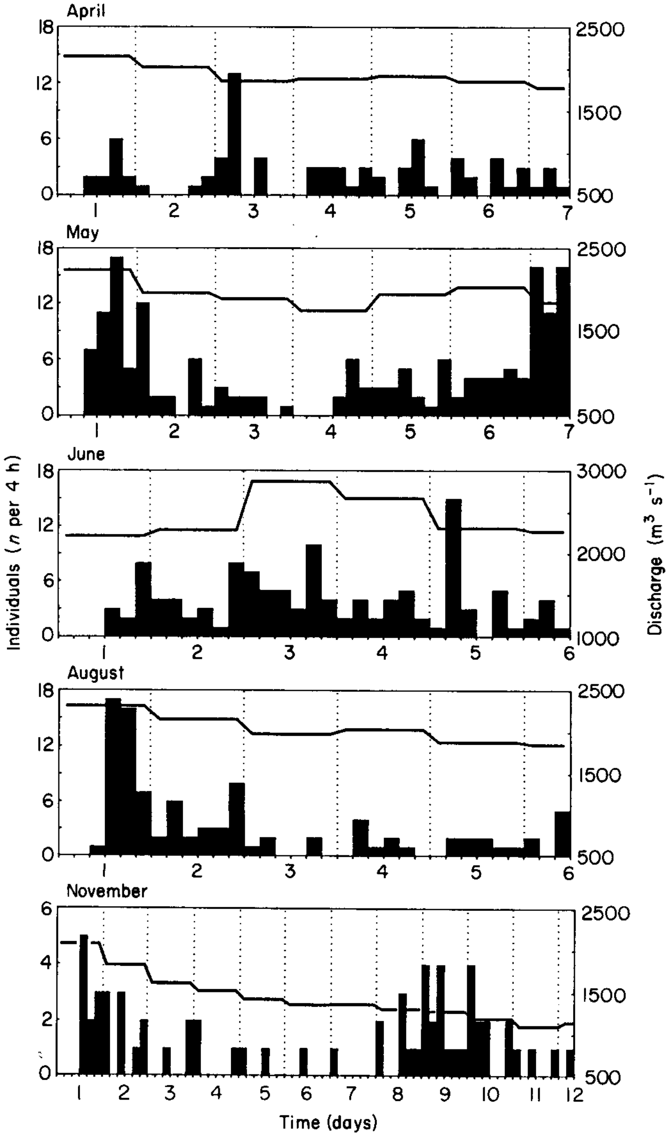

FIG. 3. Temporal pattern of number of macroinvertebrates (n) in the drift, taken continously (each sampling period was 4 h) over several days: (——) mean daily discharge ($m^3 s^{-1}$); (. . . .) midnight.

In order to establish a diel rhythm, all drifting animals sampled in the same 4-h interval in the whole period (April–November) were summed, because of the low numbers in each period. No marked diel rhythm could be detected, but the Oligochaeta seem to show a nocturnal maximum, the Crustacea appear to have a peak during dusk and the Diptera larvae one in the afternoon (Fig. 4). But care must be taken when interpreting these general patterns because of the summing up of the data from different periods and the difficulties in the timing of the samples (see Methods).

Discussion

Quantification of drift in large rivers has not received much attention because sampling problems have greatly limited such studies. Until now, drift samples in large rivers were

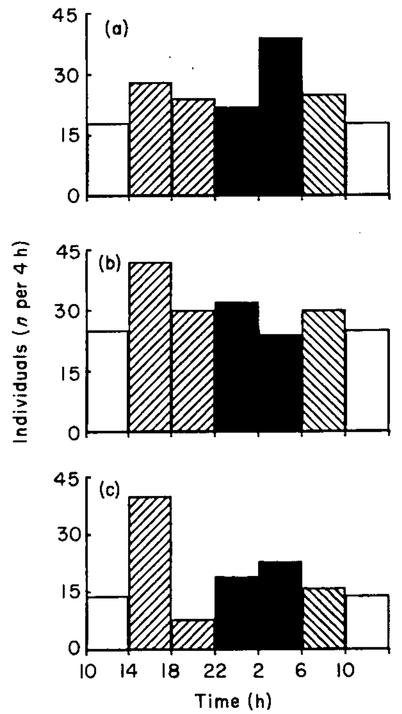

FIG. 4. Diel drift pattern of major groups of macroinvertebrates (overall April–November 1989). Ordinate: number of individuals taken over a period of 4 h. Abscissa: time (sampling interval = 4 h). ■, Night; ▨, periods with dusk or dawn; □, day. (a) Oligochaeta; (b) Crustacea; (c) Diptera-larvae.

obtained by using nets or colonization samplers (e.g. Berner, 1951; Obi & Conner, 1986; Cellot, 1989), the exception being Liakhov & Zhidkov (1953) using a bottom tray sampler for studying the drift in the River Volga. These methods are very selective to certain groups of macroinvertebrates and restrict sampling to appropriate environmental conditions. The new apparatus in this study samples continuously for up to 14 days and its performance in the river is largely independent of environmental conditions.

The qualitative and quantitative descriptions of the macroinvertebrate drift, using a single sampler at only one site, as in the present study, may be influenced by the horizontal and vertical distribution of animals in the channel of a large river (e.g. Matter & Hopwood, 1980; Statzner, Dejoux & Elouard, 1984). The comparison between bottom and surface drift samples studied on one occasion showed slight, but just significant, differences. In contrast, the spatial distribution of real or flow-weighted catches in streams and small rivers often follows a Poisson series, with quantitatively similar samples (Elliott, 1970; Hemsworth, 1979).

Benthos surveys in the Danube recorded ninety-two taxa (Appendix) and 57% of the taxa found in the drift were present in the benthos samples, the most notable exceptions being several species of the chironomids. Almost 50% of the taxa found in the drift have already been reported in previous studies (e.g. Bournaud & Thibault, 1973; Adamus & Gaufin, 1976; Statzner, Dejoux & Elouard, 1984; Grzybkowska, Pakulska & Jakubowski, 1987) and twenty-five taxa were recorded in the drift for the first time (see Table 2).

More than 50% of these drifting macroinvertebrates belonged to groups of animals which behave in a similar way to dead animals in the drift (e.g. Oligochaeta, Mollusca and Diptera larvae) (Elliott, 1971a). It is believed that these animals are removed from the drift by chance effects. The remaining groups (e.g. Crustacea, Ephemeroptera and Trichoptera), which are less than 50% of the drifting macroinvertebrates, are known to be active drifters that return to the bottom at a faster rate than dead animals (Elliott, 1971a; Elliott & Bagenal, 1972).

The downstream transport of macroinvertebrates was not constant, but varied with season, from day to day and during the course of the day. In agreement with other results from the temperate region (Waters, 1962; McLay, 1968; Clifford, 1972a, b; Hemsworth & Brooker, 1981; Koetsier & Bryan, 1989), the drift in the Danube decreased towards the winter. There were no discernible differences in the 4-h values of continuous samples up to 12 days for the fauna as a whole, regardless of the season and environmental conditions, e.g. low or high discharge levels, and the differences between the numbers of animals that drifted during day hours and during night hours were not significant. This is in contrast to other results, where seasonal drift patterns were markedly influenced by flow changes (e.g. Radford & Hartland-Rowe, 1971; Irvine, 1985). Drift during droughts and spates was not studied in the present investigation. The large temporal variation in numbers, obtained from the continuous samples (Fig. 3), showed that estimates of the number of drifting animals obtained from short-term investigations might be misleading.

TABLE 4. Summary of information on the drift–benthos ratio in streams and rivers with different levels of discharge (including information available for large rivers): showing the locality, country, and period where the variables were studied, mean discharge (with range), the width and depth of the river (with range); the method with which drift was sampled and the mesh size of the drift net; the organisms included in the drift counts (total = no differentiation in faunal groups); mean drift density in numbers per $100 m^3$ (with range; calculated through drift rate and discharge with time interval); mean benthos density (with range) in numbers per m^2; the drift rate in numbers per day per river section in millions (with range; calculated through the range either of discharge or drift density); mean ratio of numbers of individuals in the drift to that of the benthos in % (with range; calculated through the range either of benthos or drift density). The rivers are grouped according to their mean discharge ($m^3 s^{-1}$). (A) Austria; (AUS) Australia; (CDN) Canada; (CSFR) Czechoslovakia, (G.B.) Great Britain, (F) France, (ML) Malaysia, (N.Z.) New Zealand, (PL) Poland, (S) Sweden, (U.S.A.) United States of America, (U.S.S.R.) Union of Socialist Soviet Republics

River (Country)	Study period	Mean discharge in $m^3 s^{-1}$ (with range)	Width (m) (range)	Depth (m) (range)	Method	Mesh size (μm)	Fauna[a]	Drift density (no. $100 m^{-3}$)	Benthos density (no. m^{-2})	Drift rate[b] (numbers day) in millions	Drift–benthos ratio (%)	References
Walla Brook (G.B.)	Jun 63– Oct 64	–	1.96 (1.1–4)	0.29 (0.18–0.5)	net	440	benthos	45.6* (22.1–86)*	6327 (2330–10815)	0.0007 (0.0002–0.002)	0.0018 (0.0002–0.0086)	(1)
Jetty Noone Mapourika (N.Z.)	Nov 84– Mar 86	0.019 0.045 0.083	0.8 1.2 2.3	–	net	250	benthos	–	500 1300 650	–	(<0.001–0.009)	(2)
Loucka Creek (CSFR)	May 65– Dec 66	–	–	0.15	tube	–	benthos	30350[c] (1000–122000)	max 3162	–	2.4 (0–41.2)	(3)
Waitaki (N.Z.)	Mar 83– Apr 83	0.075	3	0.19 (0.1–0.3)	net	425	benthos	1280 (860–1520)	11182.5 (4300–22450)	0.083* (0.056–0.098)*	0.014 (0.011–0.019)	(4)
Dale Park Beck (G.B.)	Apr 70– May 71	0.34 (0.06–0.72)	(3–3.5)	0.19 (0.14–0.25)	net	440	benthos	27.6* (4–62.5)*	2278*[d] (2196–2360)*	0.008* (0.001–0.017)*	0.0023* (0.0022–0.00239)*	(5)
Yuccabine Creek (AUS)	Apr 83– June 84	–	(3–8)	0.3 (0.1–0.5)	net	500	total	126 (36–398)	2403 (830–4478)	–	0.0157* (0.0084–0.0456)*	(6)
Bere stream (G.B.)	Jul 66	0.42	8	0.3	pipe	500	benthos	191.7	4711	0.070	0.0122*	(7)
Island (N.Z.)	Dec 64– Dec 65	–	9	0.2 (0.1–0.3)	net	–	benthos	549.2 (141–857)	11327	–	0.01* (0.0025–0.0151)*	(8)
Mill stream (G.B.)	Oct 65– May 66	0.71 (0.46–5.8)	8	0.7	pipe	500	benthos	91.2	11850 (5500–27000)	0.056 (0.036–0.458)*	0.0054* (0.0024–0.0116)*	(7)
Gombak (ML)	Oct 68– Nov 69	1.0 (0.04–3.16)	6 (2–12)	0.18 (0.1–0.3)	net	165× 560	benthos	134.4 (47.9–701)	2753 (980–5130)	0.119 (0.007–0.35)	0.01595 (0.0038–0.0405)	(9)
Tees (G.B.)	Jul 70– Sep 73	1.29* (0.45–3.98)	(20–30)	<1	pump net	275 440	benthos exc. *Hydra*, *Nais*	393.6 49	2186[e] (950–6260)	0.439* 0.055*	(0.0315–0.2076)*[f] (0.0039–0.0258)*[f]	(10)

Speed (CDN)	Jul 66– Dec 66	(0.1–20)	(5–10)	(0.08–0.15)	net	167× 560	insects	(5.8–1161.4)*	349 247 (76 198–950 992)	0.10 (0.0204–0.257)	0.00118 (0.00021–0.0037)	(11)
Wye (G.B.)	Mar 75– Feb 76	–	(8.2–17.6)	(0.25–0.54)	net	440	benthos	–	max 3057	(0.034–0.798)	0.03434 (0.006–0.1096)[g]	(12)
Blackwater Creek (U.S.A.)	Dec 71– Dec 72	2.86 (0.02–32.5)	(8–10)	0.25	net	470	total	16.0 (3–49)	435.5	0.04* (0.0003–0.449)*	0.00919* (0.00172–0.0281)*	(13)
Widawka (PL)	Mar 83– Mar 84	5 (–8.5)	(24–29)	0.85 (0.8–0.9)	net	120– 1000	total	234 (36–522.3)	7364 (2836–17 303)	1.01* (0.16–2.3)*	0.027* (0.011–0.07)*	(14)
Tjulån (S)	Jul 61– Oct 66	27.6 (6.9–55.6)	20 ,, (15–25)	0.3 (0.1–0.5)	net	145	benthos	599 (358–913)	667 (91–1289)	5.899 (2.63–9.05)	0.2701* (0.1396–2.0150)*	(15)
Satilla (U.S.A.) upper site lower site	Dec 74– Dec 75	44.7 (2.9–280) 87.2 (6.9–504)	–	(1–>4)	net	400	total	335.3 238.7	30 000	12.9* (0.84–81.12)* 17.98* (1.42–103.94)*	–	(16)
Upper Rhône (F)	Dec 78– Mar 80	510 (250–2000)	150	4 (3–5)	net, sas[h]	500	benthos exc.*Hydra*	100 (2.7–197)	(1700–9200)	44.1 (21.6–172.8)*	(0.0435–0.236)*	(17)
Upper Mississippi (U.S.A.)	Jun – Jul 81	892.5	–	(3.5–7)	net	595	total exc.plankton	71.3	–	55.0*	–	(18)
Middle Missouri (U.S.A.)	Apr 76– Nov 76	909.4 (704–1259)	–	–	net	571	total	41.4 (7–395)	1705.8* (6–14 496)	32.509* (5.5–310.36)*	–	(19)
Lower Missouri (U.S.A.)	May– Oct 45 (? 46)	1671	(457–1609)	–	net	–	total	44.3*	19.7	64.0	–	(20)
Danube (A)	Apr – Nov 89	1846 (723–6949)	330	(1.9–4.0)	continuous net	400	benthos	18.5 (12.5–31.3)	19 360	13.6	0.0038 (0.0026–0.0064)	(21)
Lower Mississippi (U.S.A.)	Apr – Aug 77	4500[i]	900	(2.1–20.4)	net	505	total	83.3 (64–112)	–	323.9* (248.8–435.5)*	–	(22)
Volga (U.S.S.R.)	Jul 52	–	–	–	[j]	–	benthos	(400–7700) ?	–	49.9	–	(23)
Volga[k] (U.S.S.R.)	May 53– Jun 54	17 620 (5860–30 100)	–	–	[j]	–	benthos exc.*Hydra*	219.8 (70.3–463.6)	–	2999.9* (907–7873.6)*	–	(24)

*Calculated from the data in papers with given river depths.

[a]Fauna in the drift related to benthos; [b]estimated for the whole river section; [c]including microdrift ?; [d]calculated from the geometric mean; [e]data for densities of benthos for the years 1972 and 1973 only; [f]assumption for calculation (Elliott, 1967) = a mean depth of 0.5 m; [g]calculated from the formula (Hemsworth & Brooker 1979) $P\% = x.100.D/X$ where x = individuals m^{-3}, D = depth (m), X = individuals m^{-2}); [h]suspended artificial substrate; [i]value given by Cellot (1989); [j]apparatus for sampling drift near the bottom; [k]data during spates.

References: (1) Elliott, 1967; (2) Graesser, 1988; (3) Kubicek, 1969; (4) Irvine, 1985; (5) Elliott & Bagenal, 1972; (6) Benson & Pearson, 1987a,b; (7) Crisp & Gledhill, 1970; (8) McLay, 1968; (9) Bishop, 1973; (10) Armitage, 1977; (11) Bishop & Hynes, 1969a; (12) Hemsworth & Brooker, 1979; (13) Cowell & Carew, 1976; (14) Grzybkowska, Pakulska & Jakubowski, 1987; (15) Ulfstrand, 1968; (16) Benke, Hunter & Parrish, 1986; (17) Cellot, 1989; (18) Eckblad, Volden & Weilgart, 1984; (19) Carter, Bazata & Andersen, 1982; (20) Berner, 1951; (21) present study; (22) Obi & Conner, 1986; (23) Liakhov & Zhidkov, 1953; (24) Liakhov, 1961.

No marked diel rhythm could be detected for the groups considered: Oligochaeta, Diptera larvae and Crustacea. Although the Oligochaeta are not known to be animals with a marked diel activity pattern, one should use caution when judging general activity patterns from pooled seasonal day–night values, especially for heterogenous taxa such as chironomids, as seasonal changes in activity could smooth the pattern in the pooled values. One key factor, responsible for the absence of a diel activity pattern, is the low light intensity. In the Danube, at a depth of 3.5 m and between 10 and 20 mg of suspended particles l^{-1}, 99.54–99.94% of the light is absorbed in the water column (Dokulil, pers. comm.). The low light intensity above the bottom throughout the 24-h cycle, with no marked rhythm, could have eliminated the rhythmic periodicity of drifting macroinvertebrates. The absence of a diel periodicity in the drift has been reported for several macroinvertebrates under continuous dark conditions (e.g. Elliott, 1965; Haney *et al.* 1983).

Despite the scarcity of information on drift in large rivers, the information available for streams and rivers is summarized in Table 4. Although a detailed comparison with other studies is difficult, because the methods, analyses and fauna are often very different, the comparison clearly shows that drift densities vary widely from place to place. High values were reported from streams with a discharge $<100\,m^3\,s^{-1}$ and low values for large rivers (e.g. Danube) and density dependent and independent factors have been considered to explain differences in drift density (summarized by Statzner, Dejoux & Elouard, 1984; Brittain & Eikeland, 1988). As the mean benthos density ranged from about 19.7 to 349 247 animals m^{-2}, the mean proportion of total benthos drifting at any instant in time ranged from about 0.00118 to 2.4% and the values for the Danube were in this range. Although most of the values in Table 4 are low, these movements often amount to a daily drift over a unit area of stream or river bed of many times the quantity of organisms in that area (Waters, 1972). Therefore, when the proportion of the population entering the drift per unit area per day was calculated, values of 4.3% (Elliott, 1971a), 3.6% (Townsend & Hildrew, 1976) and 12–204% (Hemsworth & Brooker, 1979) were found.

The estimated rate of the total macroinvertebrate drift in the Danube was about 13 600 000 animals per 24 h; this value is in the range of that for large rivers, and in comparison to streams or small rivers it reflects the relationship between this rate and that of the discharge. The latter relationship could be described by a power function in agreement to, e.g. Elliott (1971a), Zelinka (1976) and Crisp & Robson (1979), but changes in the total number estimated to be drifting reflected seasonal changes in drift density rather than changes of the stream flow in the upper Wye (Hemsworth & Brooker, 1981).

Mean distances travelled and distances travelled by 1%, 10% and 50% of the macroinvertebrates were calculated as a rough estimate for downstream transport (Table 5). For the two groups of animals mentioned earlier, the mean distance travelled ranged from about 4 m to 31 m and the distance travelled by 1%, 10% and 50% of the animals from about 3 m to 139 m, dependent on the water velocity, but downstream population displacement over the aquatic phase of the life cycle was not estimated. Hemsworth & Brooker (1979) calculated a distance of 10 km for such a displacement. Therefore, the downstream movement in the river current of large numbers of macroinvertebrates clearly profoundly influences benthic community dynamics in two ways. Firstly, the continuous loss of animals into the water column reduces benthic density and, as some species and size-classes are more prone to drift than others, the composition of the local community is affected. Secondly, the continuous settling out of animals from the drift plays an important colonizing role.

Thus, the twin influences of drift contribute to the continuous (re)distribution of benthos (Townsend & Hildrew, 1976). Bearing in mind, that the Danube at Altenwörth is impounded for hydroelectric purposes, and assuming that 4% of the population might enter the drift per day and drift distances travelled are about 4–31 m, it seems obvious that drift plays an important part by colonizing the area above the barrage, as colonization from downstream is probably only possible through the water passages for ships and through the upstream flight of the mature females of aquatic insects. As the major groups in the drift, Oligochaeta and Diptera larvae, are not known to show upstream movement (Söderström, 1987) and upstream movement as a whole compensates for only 2–39% of the number drifting downstream (Bishop

TABLE 5. Estimates for mean drift distances and distances travelled by 1%, 10% and 50% of macroinvertebrates. Calculated from $X = a\ V^{b_1}$ and $X_P = A_P\ V^{b_2}$ respectively, where X is the mean drift distance (m) and X_P the distance travelled by P%, V is the mean water velocity (cm s^{-1}) (see Table 1), using the constants a, A_P and b_1, b_2 from Table 6 in Elliott (1971) for group 1 (not different from dead animals, e.g. Oligochaeta, Mollusca, Diptera larvae) and group 3 (different from dead animals, e.g. *Hydropsyche*, *Gammarus*)

	Mean drift distance (m)					Distance travelled (m)													
	Constants		Water velocity (cm s^{-1})			Constants				Water velocity (cm s^{-1})									
	a	b_1	40	70	90					40			70			90			
						A_{P1}	A_{P10}	A_{P50}	b_2	1%	10%	50%	1%	10%	50%	1%	10%	50%	
Group 1	0.3098	1.0174	13.75	24.30	31.39	1.4267	0.7134	0.2148	1.0174	60.85	30.43	9.16	107.53	53.77	16.19	138.86	69.44	20.91	
Hydropsyche	0.1815	1.0625	9.14	16.57	21.64	0.8358	0.4179	0.1258	1.0625	42.10	21.05	6.34	76.30	38.15	11.48	99.65	49.83	15.00	
Gammarus	0.1015	0.9770	3.73	6.44	8.24	0.4674	0.2337	0.0704	0.9770	17.18	8.59	2.59	29.67	14.84	4.47	37.93	18.97	5.71	

& Hynes, 1969b; Elliott, 1971b; Williams & Moore, 1982), it is likely that drift is an essential cause for the high density of macroinvertebrates, e.g. Oligochaeta and chironomid larvae, in the area above the barrage (Humpesch, 1989) and for recolonization of this area after spates. [In spates the sluices will be opened, the water of the impoundment is gradually released to a certain level taking parts of the bottom substratum and the fauna downstream and therefore standing stock is reduced or eliminated. After spates the sluices are closed again, the release stops and sedimentation and recolonization can occur (Prazan, 1990).]

To confirm these theoretical considerations, more detailed work is necessary on drift of an impounded large river, such as the Danube.

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Appendix

Taxa of the benthic macroinvertebrates occurring in the Danube at river kilometre 2005, 30 m from the right bank. Study period from October 1986 to December 1987 (Petto, Humpesch & Anderwald, 1991).

Mollusca:
Ancylus fluviatilis Müller, *Bithynia tentaculata* (Linn.), *Gyraulus albus* (Müller), *Potamopyrgus jenkinsi* (Smith); *Dreissena polymorpha* (Pallas), *Pisidium henslowanum* (Sheppard), *P. nitidum* Jenyns, *P. subtruncatum* Malm, *P. supinum* Schmidt, *Sphaerium corneum* (Linn.).
Polychaeta:
Hypania invalida (Grb.)
Oligochaeta:
Chaetogaster diastrophus (Gruithausen), *Nais alpina* Sperber, *N. bretscheri* Mich., *N. communis* Piguet, *N. elinguis* Müller, *Propappus volki* (Mich.), *Stylaria lacustris* (Linn.), *Stylodrilus heringianus* Clap.; Tubificidae.
Hirudinea:
Erpobdella octoculata (Linn.), *Glossiphonia complanata* (Linn.).

Other invertebrates (except insects):
Dendrocoelum lacteum (Müll.), Tricladida; Acari; *Jaera istri* Veville; *Chaetogammarus tenellus* Sowinskyi (Behning), *Dikerogammarus haemobaphes fluviatilis* Martinov, *Corophium curvispinum* Sars.

Insecta
Ephemeroptera:
Baetis sp., *Ephemerella ignita* (Poda), *Heptagenia sulphurea* (Müll.).
Coleoptera:
Elmis sp.
Trichoptera:
Brachycentrus subnubilus Curtis, *Ceraclea* spp., *Hydropsyche pellucidula* Curtis, *Hydropsyche* spp., *Lepidostoma hirtum* Fbr., *Oligoplectrum maculatum* Fourcroy, *Psychomyia pusilla* Fbr.
Diptera, Simuliidae:
Boophtora erythrocephala (de Geer), *Simulium columbaschense* (Fabr.), *S. galeratum* Edw., *Simulium* sp.
Chironomidae:
Brillia longifurca (Kieffer), *Cladotanytarsus mancus* (Walker), *Conchapelopia* sp.1 Fittkau, *Cricotopus albiforceps* (Kieffer), *C. annulator* (Goetghebuer), *C. bicinctus* (Meigen), *C. festivellus* grp. I/II (Meigen), *C. tremulus* grp. (Linn.), *C. triannulatus* (Macquart), *Dicrotendipes* cf. *nervosus* (Staeger), *Eukiefferiella brevicalcar* (Kieffer), *E. claripennis* (Lundeck), *E. clypeata* (Kieffer), *E. gracei* (Edwards), *E. lobifera* (Goetghebuer), *E. tirolensis* (Goetghebuer), (*E.* grp. *claripennis*), *Micropsectra* sp.1 Kieffer, *M.* sp.2 Kieffer, *Nanocladius rectinervis* (Kieffer), *Orthocladius* cf. *excavatus* (Brundin), *O.* cf. *frigidus* (Zetterstedt), *O.* cf. *saxicola* (Kieffer), *O. rivicola* (Kieffer), *O.* sp.1 a (Schmid), *O.* sp.D (Schmid), *O. thienemanni* (Kieffer), *Parachironomus* cf. *frequens* (Malloch), *Parakiefferiella* sp.1 (Thienemann), *Parametriocnemus stylatus* (Kieffer), *Paratanytarsus* sp.2 Thienemann & Pause, *Paratrichocladius rufiventris* (Meigen), *P. skirwithensis* (Edwards), *Polypedilum* grp. *laetum* I (Meigen), *P.* grp. *nubifer* (Skuse), *P.* grp. *pedestre* (Meigen), *Potthastia* cf. *pastoris* (Edwards), *Rheocricotopus chalybeatus* (Edwards), *Rheopelopia ornata* (Meigen), *Rheotanytarsus* cf. *curtistylus* (Goetghebuer), *Smittia edwardsi* (Goetghebuer), *Synorthocladius semivirens* (Kieffer), *Tanytarsus* sp.1 van der Wulp, *Trissopelopia* sp.1 Kieffer, *Tvetenia calvescens* (Edwards), *T.* cf. *discoloripes* (Goetghebuer), *T.* sp.A (Cranston), *T.* cf. *veralli* (Edwards).