

## Spatial and temporal distribution of the zoobenthos community in a woodland pond (Switzerland)

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### Abstract

Spatial and temporal changes of zoobenthos composition and density were assessed in a woodland pond, near Geneva (Switzerland), by monthly sampling (during 15 months), on the three main substrates: a submerged macrophyte (*Chara* sp.), an emergent macrophyte (*Typha latifolia* stems) and allochthonous detritus (oak leaves).

Many taxa showed preferences for one or two of the substrates, as expressed by differences in densities, but few taxa presented an exclusivity for one substrate. Zoobenthos densities (per m<sup>2</sup> of pond bottom) were largely dominated on all substrates and seasons by Chironomidae and Oligochaeta. Other dense macroinvertebrates included Ostracoda (on *Chara* and *Typha* stems), Gastropoda (on *Typha* stems), Ephemeroptera (all substrates), and Ceratopogonidae (on *Typha* stems).

The magnitude of temporal differences in densities was expressed by the ratio of maximal to minimal monthly densities and reached values between 2.8 to 11.8. On all substrates the highest monthly densities were observed in summer or beginning of autumn. The temporal changes in densities were strongly influenced by the life cycles of the invertebrates: presence of numerous young individuals in summer (for example *Cypridopsis vidua*, *Cloeon dipterum*, *Caenis horaria*, *Ferrissia wautieri*), and emergence (for example Chironomidae in April). Fluctuations in densities, especially on *Chara* and leaves, were also attributed to modification of substrate condition (surface availability, stage in the decomposition or senescence process). Temporal fluctuations of densities were compared with other lentic water bodies: highest densities showed a common trend, occurring between end of spring and beginning of autumn.

### Introduction

Space and time are of central importance in every ecological investigation. Limitation of scale in space or in time, often leads to only a brief and often dim glimpse of the relevant processes (Wiens *et al.*, 1986). There is a need for studies focusing on the effects of these two factors (space and time). Knowledge of spatial and temporal distribution patterns allows a reduction of bias in the analysis of data collected and permits the elaboration of sampling strategies. Such information is particularly needed for the zoobenthos of poorly studied systems like ponds. This type of water body usually offers a mosaic structure determined mainly by macrophytes and allochthonous plant material. Similar structural patchiness is also frequently found in former

river channels, littoral zones of lakes or large rivers, estuaries, marshes and swamps.

Space and time are two factors inducing changes in a zoobenthos community. The changes can either concern faunal composition, species richness and diversity, abundance, biomass or productivity. Previous reviews (Minshall, 1984; Ward, 1992) have presented some key factors (abiotic or biotic) leading to spatial patchiness: type of substrate, temperature, flow regime, chemical composition of water, light, food, current, oxygen, and interaction with other organisms. Spatial distribution of macroinvertebrates is particularly influenced by macrophyte community composition and distribution (e.g. Kreckler, 1939; Korinkova, 1971; Soszka, 1975a; 1975b; Biggs & Malthus, 1982; Dvorak & Best, 1982; Scheffer *et al.*, 1984; Lodge,

1985; Castella, 1987; Cyr & Downing, 1988). Spatial patterns in the chosen pond will be investigated by the comparison of macroinvertebrate densities occurring on the three main plant substrates: *Chara*, *Typha* stems, and allochthonous leaf litter. Temporal variations in fauna can exist at scales ranging from minutes to years (Minshall, 1984). In the present study I will investigate temporal variations in macroinvertebrate densities in terms of monthly changes.

My aim is to describe and analyze the magnitude and effects of temporal and spatial heterogeneities in zoobenthos densities of a pond, and further to propose recommendations about methodology of zoobenthos survey in this kind of water body.

### Study site

This study was conducted in a recent man-made pond (created in 1969). The 'Bois-Vieux' woodland pond is situated on an argillaceous moraine in a forest near Geneva (Switzerland) (493 m a.s.l.). It had an area of 4400 m<sup>2</sup> and a mean depth of about 0.8 m (max.: 2 m). The water inputs were rainfall, surface run-off and a small forest inlet. The pond discharged through an outlet. Water level fluctuations were moderate ( $\pm 0.2$  m). The mean annual temperature (1989) of the water was 12.7 °C (extreme values: 3 °C [January] and 23 °C [July–August]), and accumulated degree-days were 4633; the temporal fluctuation of the temperature has been presented by Oertli (1993).

Conductivity, and concentrations of calcium, chloride, sulfate, phosphorus, nitrate, nitrite, and ammonium nitrogen were low, and the pH was slightly basic (7 to 8) (Auderset *et al.*, 1993). Dissolved oxygen concentrations were mostly below saturation (60–90%), but some high values (200%) occurred in *Chara* beds during sunny summer days.

The main substrates were leaf litter (25% of pond area), *Chara* sp. beds (*C. vulgaris* L. and a small proportion of *C. globularis* Thuillier) (13% of pond area) and *Typha latifolia* L. (28% of pond area) (Fig. 1). In the area of dense *Chara*, where macroinvertebrates were sampled, mean annual biomass of *Chara* was estimated at around 200 g m<sup>-2</sup> (dry mass), with the highest values in summer (around 330 g m<sup>-2</sup>) and lowest in winter (around 80 g m<sup>-2</sup>). The *Typha* area showed a mean depth of 0.5 m, and stem density was estimated at 41 ( $\pm 10$ ) stems per m<sup>2</sup>. About half of the stems were green (current generation) and the other half were brownish (generation one year older).

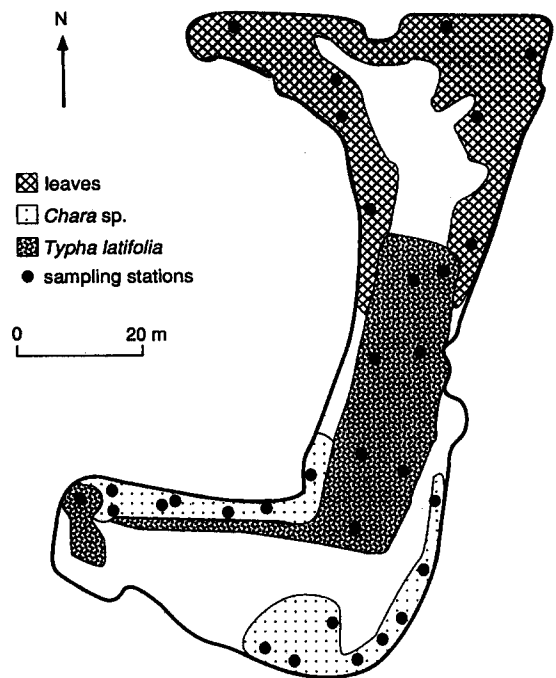


Fig. 1. Spatial distribution of main substrates (leaves, *Chara*, *Typha*) in 'Bois-Vieux' pond, and location of sampling stations.

The populations of vertebrate predators were relatively scarce, and comprised tadpoles, newts, fishes and shrews.

### Methods

The macroinvertebrate sampling strategy (methods, number of samples) was chosen after a preliminary study carried out in the summer of 1988. A stratified-random sampling design was used to select the permanent sampling stations (see Fig. 1).

#### Leaf litter

To sample this substrate, leaf mesh bags were introduced. The bags contained 4.85 g dead oak leaves (*Quercus robur* L.) (dried at 60 °C to constant mass). This quantity simulated the mass per unit of area of natural accumulation in the pond, as estimated by some surveys. Two mesh sizes were used: fine (5 mm) and coarse (12.5 mm), but no subsequent differences were recorded in faunal composition. Bags were immersed during natural leaf fall on 8–9th November 1988 (64 bags of each type) and on 7th November 1989 (32 coarse mesh bags). The bags were equally distributed

(depth of about 35 cm) among 8 stations. The fine and coarse mesh bags occupied a bottom surface of 150 and 200 cm<sup>2</sup> respectively.

Eight bags (four of each type) were removed monthly between January 1989 and December 1989, except in summer (May to July) when sampling was bimonthly. In 1990, one sampling occurred in March. Bag contents were preserved in 4% Formalin. In the laboratory, the leaves were washed through a 0.25 mm mesh sieve, dried (60 °C to constant mass) and weighed. Macroinvertebrates were identified, counted, grouped by size class, and preserved in Formalin. Sub-sampling was used for some dense macroinvertebrates: Chironomidae, Oligochaeta and Ostracoda. Oak leaves decomposition was slow (Oertli, 1991), and mean dry weight per pack was 4.08 g ( $\pm 0.19$ ) in January, 2.36 ( $\pm 0.91$ ) in July and 1.6 ( $\pm 0.99$ ) in December.

Mean annual densities (1989) were expressed on a pond bottom surface basis (m<sup>2</sup>), and were the arithmetic means of monthly densities; they are presented with 95% confidence limits calculated by multiplication or division with the factor derived from the log transformation (Elliott 1977, for small samples from contagious distribution) of  $n$  annual means in the  $n$  sampling locations:

$$\text{antilog}\left(t\sqrt{\frac{\text{variance of transformed means}}{n}}\right)$$

The annual densities were calculated from bags immersed in November 1988 (sampled between January and November 1989) and in November 1989 (sampled in December 1989).

#### *Chara and Typha*

Fifteen samples of *Typha* stems (seven or eight from each generation of stems: the current and the one year older) and 15 of *Chara* were taken monthly from January 1989 to December 1989. In 1990, sampling occurred at the end of January and in March.

Cores (40–50 cm high and 4.4 cm diameter) were used for sampling the submerged part of *Typha* stems. The aerial part of the plant was cut at water level; this procedure could induce the escape of swimming species, and therefore was implemented one day before sampling. On a sampling day, the marked remaining submerged stems were quickly enclosed in the core and cut at approximately 35 cm under the water level. A part of the *Chara* bed was rapidly enclosed with a plastic box (10 × 9 × 9 cm) and a lid at a depth of about 35 cm. The mean *Chara* mass (dried at 105 °C)

obtained was 3.3 g per sample. Preservation and laboratory procedures were the same as for the leaves.

## Results

The total area sampled was 16.5 m<sup>2</sup> and provided 625 500 invertebrates belonging to 113 taxa (identification levels as presented in Table 1, completed by rare taxa listed in Oertli [1992]).

### *Spatial patterns*

Annual mean densities of dominant macroinvertebrates on the three substrates are presented in Table 1. From the 39 listed taxa, only the most numerous (*i.e.* with densities higher than 30 ind. m<sup>-2</sup> on one of the substrates) are kept for discussion.

The highest annual total density occurred on *Chara* and the lowest on *Typha* stems. Chironomidae and Oligochaeta dominated on all substrates, but with a lower magnitude on *Typha* stems. Other dense macroinvertebrates included Ostracoda (on *Chara* and *Typha* stems), Gastropoda (on *Typha* stems), Ephemeroptera (all substrates), and Ceratopogonidae (on *Typha* stems). A major feature of the spatial distribution was that most of the dominant taxa showed a preference (more or less marked) for one of the three substrates; few taxa seemed indifferent to substrate type. The preferences were highlighted by important differences in densities, but rarely by absence from a substrate. The most conspicuous spatial heterogeneities were as follow. Five taxa were present mainly on *Typha* stems: *Ferrissia wautieri*, *Donacia vulgaris*, *Noterus clavicornis*, Dixidae and Limoniidae. This substrate bore a relatively low density of: *Gammarus pulex*, Odonata, *Sialis lutaria* and *Caenis horaria*. Six taxa were clearly more dense on *Chara* than on the two other substrates: Hydridae, *Gyraulus crista*, *Cypridopsis vidua*, *Cloeon dipterum*, *Haliplus obliquus* and *Athripsodes aterrimus*. Two taxa avoided the *Chara*: *Ferrissia wautieri* and *Helobdella stagnalis*. One taxon, *Cyrnus trimaculatus*, showed a clear association with leaves, whereas the Acarina avoided this substrate.

### *Temporal patterns*

Changes in the monthly total densities of macroinvertebrates during the studied period are presented for the three substrates in Fig. 2 (upper panel); these densities

Table 1. Annual macroinvertebrate densities (1989), associated 95% C.L. factor, and relative contribution to total, on three substrates (*Typha* stems, *Chara*, leaves) of 'Bois-Vieux' pond. a: adult, l: larvae.

	<i>Typha</i>			<i>Chara</i>			Leaves		
	ind m <sup>-2</sup>	95% C.L. x/÷	%	ind m <sup>-2</sup>	95% C.L. x/÷	%	ind m <sup>-2</sup>	95% C.L. x/÷	%
HYDRIDAE	3		0.04	290	1.51	0.28	12.6		0.02
MOLLUSCA									
<i>Ferrissia wautieri</i>	859.7	1.49	10.17	12.8		0.01	274.8	2.91	0.53
<i>Gyraulus crista</i>	39.6	1.92	0.47	787.7	2.12	0.71	157.8	2.19	0.31
<i>Lymnaea peregra</i>	0.6		0.01	10.3		0.01	7.5		0.01
<i>Segmentina nitida</i>	0		0.00	4		0.00	0.3		0.00
SPHAERIIDAE	0		0.00	3.6	1.08	0.00	0		0.00
OLIGOCHAETA	2771	1.34	32.77	25209	1.51	22.82	15149	1.29	29.48
HIRUDINEA									
<i>Helobdella stagnalis</i>	51.2	2.53	0.61	4.2		0.00	137.4	2.11	0.27
<i>Hemiclepsis marginata</i>	7.5		0.09	11.2		0.01	8.4		0.02
<i>Glossiphonia complanata</i>	1.2		0.01	1		0.00	2.1		0.00
<i>Theromyzon tessulatum</i>	2.6		0.03	1.4		0.00	2.1		0.00
ACARINA	229.5	1.92	2.71	164.2	1.27	0.15	5.4		0.01
CRUSTACEA									
Ostracoda: <i>Cypridopsis vidua</i>	322.4	3.13	3.81	8287	1.97	7.50	58.9	1.44	0.11
Amphipoda: <i>Gammarus pulex</i>	0.9		0.01	11.1	1.06	0.01	44.1	1.17	0.09
EPHEMEROPTERA									
<i>Cloeon dipterum</i>	360	1.46	4.26	1966	1.34	1.78	370	1.79	0.72
<i>Caenis horaria</i>	18.7	1.51	0.22	2244	1.40	2.03	1451	3.60	2.82
PLECOPTERA									
<i>Nemoura</i> sp.	7.3		0.09	4.7		0.00	1.2		0.00
ODONATA									
<i>Lestes viridis</i>	0		0.00	11.6		0.01	12		0.02
Other ZYGOPTERA §	35.6	1.70	0.42	274.2	1.40	0.25	251.9	1.43	0.49
ANISOPTERA §§	0.3	1.02	0.00	38.1	1.49	0.03	10.8	1.18	0.02
HETEROPTERA *	1		0.01	2.9		0.00	2.1		0.00
COLEOPTERA									
<i>Donacia vulgaris</i> : 1	97	1.99	1.15	2		0.00	0		0.00
<i>Haliplus obliquus</i> : 1+a	0.3		0.00	480.4	1.28	0.43	0.3		0.00
<i>Noterus clavicornis</i> : a	13.4	1.20	0.16	0		0.00	0		0.00
Dytiscidae: 1	0.4		0.00	14.4		0.01	0.3		0.00
MEGALOPTERA									
<i>Sialis lutaria</i>	0.3		0.00	10	1.06	0.01	76	1.70	0.15
TRICHOPTERA									
<i>Cyrnus insolutus</i>	155.7	1.62	1.84	122	1.87	0.11	49.3	1.36	0.10
<i>Cyrnus trimaculatus</i>	0		0.00	0		0.00	282	1.36	0.55
<i>Athripsodes aterrimus</i>	0.4		0.00	480.3	1.40	0.43	18.6		0.04
Other LEPTOCERIDAE **	0		0.00	3.4		0.00	23.9		0.05
LIMNIPHILIDAE #	20.4	1.40	0.24	14.8	1.08	0.01	53	2.06	0.10
PHRYGANEIDAE Δ	0.4		0.00	8.8		0.01	11.3	1.11	0.02

Table 1 cont..

	Typha			Chara			Leaves		
	ind m <sup>-2</sup>	95% C.L. x/÷	%	ind m <sup>-2</sup>	95% C.L. x/÷	%	ind m <sup>-2</sup>	95% C.L. x/÷	%
LEPIDOPTERA	0.9	1.02	0.01	0		0.00	0		0.00
DIPTERA									
CHIRONOMIDAE	2996	1.31	35.44	69657	1.32	63.05	32470	1.91	63.19
CERATOPOGONIDAE	358.5	1.35	4.24	326.6	1.52	0.30	435	1.62	0.85
DIXIDAE	30.5	1.63	0.36	0		0.00	0		0.00
LIMONIIDAE	42	2.08	0.50	0		0.00	0		0.00
STRATIOMYIDAE	13.9	1.82	0.16	0		0.00	0.6		0.00
Miscellaneous ##	12.6		0.15	5.2		0.00	5.3		0.01
TOTAL	8455		100	110480		100	48658		100

§ *Coenagrion puella* (more than 92%), *Ischnura elegans*, *Pyrrhosoma nymphula*, *Plactycnemis pennipes*

§§ *Cordulia aenea*, *Libellula depressa*, *Anax imperator*, *Aeshna cyanea*

\* *Sigara falleni*, *Ilyocoris cimicoides*, *Plea leachi*

\*\* mainly *Mystacides azurea*

△ *Agrypnia varia* and *Phryganea grandis*

# *Limnephilus rhombicus* and *L. flavicornis* (both dominant), *Glyptotaelius pellucidus* and *Anabolia nervosa* (scarce)

## TRICLADIDA, *Lymnaea auricularia*, *Habrophlebia lauta*, COLEOPTERA, DIPTERA

are divided into three main components: Oligochaeta, Chironomidae and other groups. The density fluctuations of the other 20 most dense taxa are presented in Fig. 2.

On all three substrates, total monthly densities were high in summer and low in winter. On leaf litter, highest total densities occurred from June to November, and were clearly lower in winter (but the minimum occurred in May). In 1989, the ratio of maximal to minimal values (= July/May) was 2.8. In *Chara* beds, total densities were high from June to October, and low in winter (minimum: January 1989). In 1989, the ratio of maximal to minimal values (= September/January) was 11.8. On *Typha* stems, total densities were greatest from July to October, and were lowest in winter (particularly in January 1989 or March 1990). A decline occurred in spring with a low value in May. In 1989, the ratio of maximal to minimal values (= September/January) was 3.4.

At the taxonomic level, the major temporal changes came from the two most dense groups: the Chironomidae and the Oligochaeta. On the leaves, both groups showed high densities in summer; in the case of the Chironomidae, high densities were still observed in autumn. On *Chara*, both groups had high densities in summer, and low in winter. On *Typha* stems, Oligochaeta attained higher densities in summer, but Chironomidae were dense in winter 1989–90. Chironomidae densities declined in May on all substrates.

Other taxa were also important in total density and were very dense during summer: *Ferrissia wautieri* and *Caenis horaria* on leaf litter, the two Ephemeroptera and *Cypridopsis vidua* on *Chara*, *F. wautieri* and *Cloeon dipterum* on *Typha* stems.

The main density fluctuations can be attributed to two factors: life cycles of invertebrates and substrate characteristics.

High densities in summer are related to the life cycle of the invertebrates and to the presence of dense newly hatched animals, as shown by population dynamics (Fig. 2), and also by size distribution (Oertli, 1992). This summer effect could be called the 'reproduction effect'. Survivorship curves of populations born in summer declined as a result of mortality, and reached low values in winter and in spring: for example *Caenis horaria*, *Cloeon dipterum*, *Ferrissia wautieri*, *Cypridopsis vidua*, *Haliplus obliquus*. Emergence of final larval stages of insects led to very low densities or absence of otherwise numerous taxa: for example *C. horaria*, *Cyrnus* spp. (June) and Chironomidae (May).

Substrate conditions (surface available, stage in the senescence or decomposition process), particularly of *Chara* and leaves, were variable, and are believed to have influenced macroinvertebrate densities. In summer, biomass of *Chara* has been estimated to be more than 4 times higher than in winter. However, in summer, the biomass of leaves was only 60% of the materi-

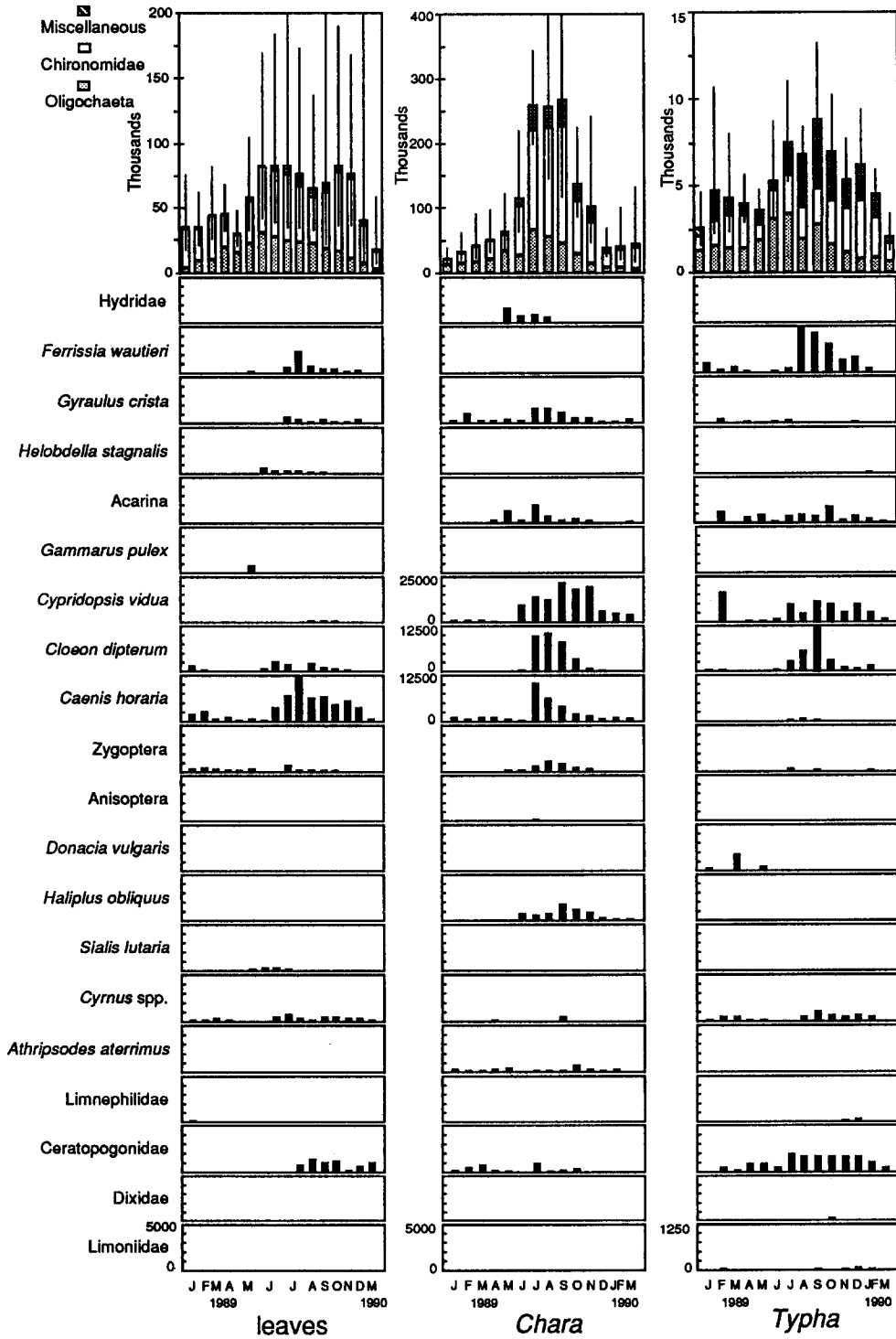


Fig. 2. Fluctuations of the monthly densities (ind. m<sup>-2</sup>) of macroinvertebrates (from January 1989 to March 1990) on the three substrates: leaves (immersed in November 1988), *Chara*, and *Typha* (older generation of stems). Upper panel: Oligochaeta, Chironomidae and miscellaneous; vertical bars represent 95% C.L. of total densities. Other panels: densest macroinvertebrates (bar charts drawn with Software GraphMu [Thioulouse, 1990]). Unless specified, all scales are the same as the lower panels (Limoniidae).

al present in January 1989, and in December 1989, only 39% remained. These changes in biomass represent changes in surface availability for macroinvertebrates. Consequently, *Chara* offered more surface in summer than in winter, and leaves offered more surface just after immersion than later. Another effect of the substrate also interfered: decomposition of this plant material, which increases attractiveness for invertebrates. Nevertheless, the effect of changes in substrate conditions is difficult to quantify in regard to invertebrate densities; each factor (surface availability or decomposition) had more or less interaction with invertebrate presence, depending on whether the invertebrate used the substrate solely as a resting place or also as a food source.

Between the beginning of 1989 and one year later, some changes in faunal densities occurred, and indicated year-to-year changes in the abundance of some populations. For example, comparisons of densities between March 1989 and March 1990 exhibited some significant differences (signed rank test). *Ferrissia wautieri* on *Typha* stems ( $p=0.003$ ), Oligochaeta on all substrates ( $p<0.05$ ), and Ceratopogonidae on *Chara* ( $p=0.015$ ) had significantly higher densities in March 1989; on the other hand, densities were significantly higher in March 1990 for *Cypridopsis vidua* on leaves ( $p=0.007$ ), Zygoptera ( $p=0.007$ ) and *Haliplus obliquus* on *Chara* ( $p=0.016$ ).

## Discussion

### *Spatial patterns*

In the studied pond, most invertebrates showed a clear preference for a particular substrate. The reasons leading to such spatial heterogeneity are numerous and have been reviewed by Minshall (1984) or Ward (1992), and will not be discussed here.

The taxa often did not show an exclusive association with the substrate: preference of a taxon could not be demonstrated by 'presence or absence' on a substrate, but more by a difference in densities. Therefore, the criterion 'presence or absence' provides only few information about spatial differences.

Differences in densities, if small, have the disadvantage of being difficult to interpret, and must always be carefully analyzed. A small difference in density, unless statistically significant, can sometimes indicate a local phenomenon which can not be generalized. Densities are often directly dependent on sur-

face availability, and indirectly on the quantity of substrate present per unit of bottom surface (for example, biomass of leaves or of macrophyte per unit area of bottom). For example, *Caenis horaria* on *Chara* and leaves showed annual densities of 2244 and 1451 ind. m<sup>-2</sup> respectively. *Chara* and leaves occurred in patches in this pond, and therefore in many places of the pond the biomass of *Chara* was lower and the amount of leaves was higher than the mean biomass estimates. This last situation would have led to the conclusion that *Caenis horaria* is more dense on leaves than on *Chara*. An objective way of dealing with this would be to establish ratios of densities; such ratios have the advantage of being independent from the unit of expression of the densities. For example the mean ratio ( $\pm$ standard-deviation) of the annual densities in each sampling station of the two main species of Ephemeroptera (*Cloeon dipterum*/*Caenis horaria*), were 16.87 ( $\pm 10.03$ ) on *Typha* stems, 1.04 ( $\pm 0.49$ ) on *Chara* and 0.62 ( $\pm 0.91$ ) on leaves. These values indicate a spatial heterogeneity of the Ephemeroptera between the *Typha* stems and the two other substrates. Other ratios (for example, *Ferrissia wautieri*/*Gyraulus crista*) also bring pertinent information on spatial patchiness, and are more objective than density differences.

### *Temporal patterns*

On all studied substrates, monthly densities fluctuated during 1989, and the highest densities occurred from June to November. The magnitude of ratios of maximal to minimal densities was around 3 on *Typha* and leaves, and 12 on *Chara*. This order of magnitude is common and was often found in various other biotopes. The time of year when total macroinvertebrate density is maximum seems to show the same broad tendency in permanent stagnant waters: all the highest densities are observed during summer, late spring, or the beginning of autumn. This trend is suggested by the present results as well as a literature survey. In the back-waters of the Upper Rhine floodplain, the highest abundances occurred between the beginning of summer and autumn, depending on sampling locality (Obrdlik & Garcia-Lozano, 1992). In *Typha* stands of a subtropical lake, strong peaks of abundance occurred in September and October (Botts & Cowell, 1993). In the Danish Lake Esrom, densities of dominant profundal invertebrates peaked in summer (Jonasson, 1972). Peak densities of the phytofauna of Polish Mikolajskie Lake occurred in summer or ear-

ly autumn (Glowacka *et al.*, 1976). In Lake Doiran (Macedonia), macroinvertebrate maximal density was observed in May (Sapkarev, 1980). In two shallow English lakes, the densest taxa (Oligochaeta and Chironomidae) generally attained their highest densities between June and October (Mason, 1977).

For some running waters, maximal densities were frequently recorded in autumn or winter (Crisp & Gledhill, 1970; Minshall, 1981; Wright *et al.*, 1983; Iversen, 1988); on the other hand, in running waters, seasonal effects are often masked by discharge effects, which makes generalization impossible. For these water bodies, contrary to stagnant permanent water, the density or biomass of macroinvertebrates is strongly influenced by discharge and flood (see for example Fisher *et al.*, 1982; Gladden & Smock, 1990; Boulton & Lake, 1992; Wright, 1992), and often seasonal density changes do not appear to show any generalized pattern (e.g. Bunn *et al.*, 1986).

The pattern of temporal density fluctuations observed in stagnant water is logically correlated with what we called here 'reproduction effect', or the presence of high densities of new-borns. This last event results from higher temperatures (air and water) and consequently from reproduction. The difference in the timing of the maximum (late spring to early autumn) depends on invertebrate community composition: some species reproduce early or late in the year, and others can be multivoltine. The common trend observed can nevertheless differ in some microhabitats, resulting from modifications of the substrate. For example, the processing and disappearance of macrophytes in winter induce migrations of macroinvertebrates, and consequently bottom substrates which bore macrophytes in summer can bear higher invertebrate densities in winter (Kornijów, 1992).

Beside the 'reproduction effect' which increases densities, two other major events also characterize seasonal patterns and lead to decreased densities: the emergence of insects and the mortality. For most populations (see Fig. 2), as a result from a continuous mortality, densities decreased rapidly after their maximum (corresponding to hatching) and were relatively low at the time of emergence. Emergence of the insects led to the absence of larvae until egg hatching. For one group of insects, the Chironomidae, emergence in late April led to a decrease in density; this decrease also affected total fauna density because of the high proportion of Chironomidae. Summer emergences may be the cause of a familiar summer minimum in standing stock of benthos (Brinkhurst, 1974), but as noticed by this

author, fish predation can also be the dominant factor in cropping the shallow bottom fauna.

In the studied pond, substrate conditions (surface availability, stage in the senescence or decomposition process) were of major importance particularly in the case of *Chara* and leaves, and influenced invertebrate densities. Decomposition of macrophytes is known to be related to an increase in macroinvertebrate densities (Smock & Stoneburger, 1980; Oertli, 1992; Botts & Cowell, 1993) or biomass (Chergui & Pattee, 1990). Invertebrates associated with leaves also respond clearly to decomposition of this substrate by modification of their densities or biomasses (e.g. Cummins *et al.*, 1989).

Comparison of zoobenthos densities from beginning of 1989 with one year later, pointed out significant differences for some taxa. In long term studies (two years or more) of permanent stagnant water bodies, such quantitative changes have often been observed (e.g. Macan, 1977; Mason, 1977; Lindegaard & Jonasson, 1979; Lindegaard, 1992). In these studies, qualitative changes in the zoobenthos composition were of minor importance; however, qualitative changes can be common during the first years of pond or reservoir existence (e.g. Barnes, 1983; Voshell & Simmons, 1984) related to colonization procedure (immigrations and extinctions).

## Conclusion

The present results, similar to others already published, point out the heterogeneities of zoobenthos structure and quantity (density) related to time or space. These two factors also affect zoobenthos food chains (Kitching, 1987; Warren, 1989).

In the studied pond, the major sources of temporal variability in zoobenthos abundance were: life cycle patterns (emergence, hatching, mortality) and substrate conditions (surface availability, stage in the senescence or decomposition process); these factors are likely to be involved in the same way in the temporal variability of numerous other analogous permanent lentic water bodies (former river channels, littoral zones of lakes or large rivers, estuaries, marshes and swamps). For intermittent biotopes (with flood and drought), water presence is another major (and sometimes dominant) cause of the temporal changes in richness and abundance (e.g. Fisher *et al.*, 1982; Boulton & Lake, 1992).

In applied studies (impact assessments and others), and also in research studies, dealing with quantifica-



tion of the zoobenthos, sampling of freshwater bodies is often avoided in winter, and reflects the avoidance of 'cold and hard' field conditions. This habit can lead to a biased view of the studied area: wrong estimation of the real annual abundance, lack of some important taxa, and false community structure. Some taxa can be missed, or densities can be overestimated or underestimated, depending upon the period of life cycle which would be sampled. Late spring, summer and autumn correspond to crucial events in life-cycle of invertebrates (emergence, hatching), and this should be kept in mind while sampling during these periods of the year. Winter seems to be a more stable period for invertebrate sampling and should be incorporated in sampling strategies. Nevertheless, this season can also have some inconveniences (such as overwintering in the egg stage for some species).

Spatial heterogeneity of substrate in stagnant water such as the studied pond, leads to heterogeneity in zoobenthos distribution. Consequently, substrate inventory and cartography should be emphasized before sampling. Nevertheless, other factors are also responsible for spatial heterogeneity in stagnant waters: for example, degree of exposure of site (e.g. Dall *et al.*, 1990), and also microconditions (e.g. Magdych, 1979; Lodge, 1986); they should also be taken into account.

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