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Seasonal dynamics and spatial distribution of chydorid cladocerans in relation to chironomid larvae in the sandy littoral zone of an oligo-mesotrophic lake

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Abstract

The seasonal variation of the principal macro- and meiobenthic taxa in the sandy littoral zone of the oligo-mesotrophic Dutch Lake Maarsseveen I was studied during two years. Population peaks of the different taxa were clearly separated in time. In early spring there were chironomid density peaks of *Stictochironomus sticticus*, in one year followed by a *Polypedilum* maximum. From June–July chydorid cladocerans dominated, with a peak of *Monospilus dispar* followed by a peak of *Rhynchotalona falcata*. In autumn the chironomid *Cladotanytarsus manicus* became dominant, remaining so throughout the winter.

To study the spatial heterogeneity of the major macro- and meiofaunal taxa, samples were taken in a grid of 2.5×10 m. Distributions of all but one taxon were significantly different from random, with Morisita indices varying from 1.23 (chironomids) to 2.10 (the chydorid *Monospilus dispar*). Wind-induced disturbance presumably had strong and species-specific effects on littoral macro- and meiobenthic taxa. Chydorid heterogeneity increased immediately following the first autumn storm of the season; this may be explained by the tendency of these organisms to remain attached to detritus particles.

Temporal and spatial correlation coefficients between macro- and meiobenthic taxa were generally low, suggesting that interactions between these groups are weak, with distribution patterns that are independent of each other. Among the meiofaunal taxa, positive spatial and temporal correlation coefficients were found; apparently, the similarity in both seasonal dynamics and spatial distribution is larger among the meiofaunal taxa than between macro- and meiofaunal taxa. Also among most of the chironomid species significant positive temporal correlations were found, except for *Stictochironomus sticticus* and *Polypedilum* sp.; these species have similar life-cycles, but were during one year temporally separated by several alternating settlement peaks. In the next year, *Polypedilum* disappeared completely following an extremely strong *Stictochironomus* settlement peak.

Introduction

The seasonal variation of benthic invertebrate density and biomass in lakes is documented in numerous studies. Typically, these focus either only on the macrobenthos (e.g. Jonasson & Kristiansen, 1967; Jonsen, 1985; ten Winkel & Davids, 1987a) or only on the meiobenthos (e.g. Whiteside *et al.*, 1978; Adalsteinsson, 1979; Holopainen & Paasivirta, 1979; Frenzel, 1982; Strayer, 1985). The contribution of the meiobenthos to the total benthic secondary production can be considerable. In one of the few lake studies available

on this subject, Strayer & Likens (1986) showed that the meiobenthos contributed more than 50% to the total zoobenthic assimilation in Mirror Lake, New Hampshire.

Much attention has been devoted to factors regulating population densities of both macro- and meiobenthos, as abiotic factors, food availability, predation and competition (e.g. Rasmussen & Kalff, 1987; Allison & Harvey, 1988; Kajak, 1988; Macchiusi & Baker, 1992). Studies from marine environments have shown that interactions between macro- and meiobenthos are potentially an important structuring factor for

benthic communities. Trophic interactions between marine macro- and meiofauna are often considered weak (e.g. Reise, 1979), with both groups operating at the same trophic level. Meiobenthic organisms may therefore compete with the macrobenthos for carbon (Lodge *et al.*, 1988). Furthermore, early juvenile stages of macrobenthic organisms are equivalent in size to the meiobenthos, and generally do rely on the same resources. Interactions between this 'temporary meiofauna' and the ambient meiofauna play an important role in marine systems (Elmgren *et al.*, 1986; Watzin, 1983; Watzin, 1986; Zobrist & Coull, 1992). The few freshwater studies available on this subject suggest that such interactions may be equally important for lake zoobenthos (McLachlan *et al.*, 1979; van de Bund & Davids, 1993). It seems reasonable to assume that benthic communities in freshwater and marine environments are structured by similar processes.

Zoobenthic organisms inhabiting the littoral zone usually are very heterogeneously distributed, both in space and in time (Elliott, 1977; Whiteside *et al.*, 1978; Gilinsky, 1984; Meire *et al.*, 1989). Spatial heterogeneity can be caused by several factors, either intrinsic (e.g. cloning, territorial behaviour, competition) or extrinsic (e.g. wind, water currents, light intensity) to the species (Ludwig & Reynolds, 1988). As a result of this heterogeneity, interpretation of quantitative field data is often difficult. The way one must deal with this problem depends upon the objective of the study. When you want to obtain an estimate of population densities at a given sampling site, it is legitimate to average out the spatial heterogeneity. When, as in this study, the objective is to study the importance of interactions between organisms and other processes occurring at the scale of an individual, this is inappropriate and can easily lead to misguided conclusions. When the distribution of a population is very heterogeneous, the majority of the individuals are concentrated in patches, experiencing much higher densities than the average population density. To obtain information about the conditions that the individual organism experiences, it is necessary to take samples at a scale relevant to the organism under study.

To quantify spatial heterogeneity, many different indices are used in literature (Elliott, 1977; Ludwig & Reynolds, 1988; Meire *et al.*, 1989; Hurlbert, 1990). Comparison of these indices is usually difficult, since it is impossible to describe spatial heterogeneity completely using one single parameter. In fact, they are all based on different definitions of heterogeneity (Pielou, 1977). To be relevant to interactions between individ-

uals, an index should be used that gives information about the chance that organisms will encounter each other. The Morisita index (I_m ; Morisita, 1971) meets this requirement very well.

In this study, the seasonal variation of the macro- and meiobenthos in the surficial sediment in the littoral zone of an oligo-mesotrophic lake was monitored simultaneously during two consecutive seasons. The objective is to describe how the population dynamics of these organisms are related, and to indicate which interactions between these organisms are potentially important. Furthermore, the spatial heterogeneity of the littoral macro- and meiobenthos of this lake was characterised, using the Morisita index, at different times of the year: once in summer, and twice in autumn, just before and just after an autumn storm likely to cause major disturbance. The study was focused on the macro- and meiobenthos living on the sediment surface and in the upper sediment layer (0–2 cm).

Description of the study site

Samples were taken from the littoral zone of Lake Maarsseveen I, a man-made oligo-mesotrophic lake located in the centre of the Netherlands near the city of Utrecht (Fig. 1). This lake has a surface area of *ca* 70 ha and a maximum depth of 32 m. The lake shore consists of *Phragmites* zones, alternated with sandy beaches. More detailed information about the study area is given in Swain *et al.* (1987). The seasonal dynamics of the macrobenthos in the sandy littoral of this lake – dominated by chironomid larvae – have been investigated extensively in the past (Ten Winkel & Davids, 1987a; Heinis & Davids, 1993). The importance of predation by bream and water mites (Ten Winkel & Davids, 1985, 1987b; Ten Winkel, 1987) and abiotic factors (Heinis & Davids, 1993) as regulating factors for these chironomid populations have been demonstrated (van de Bund & Davids, in press). A preliminary study made clear that dense populations of chydorid cladocerans dominate the littoral meiobenthos of this lake (Davids *et al.*, 1987); interactions between chironomid larvae and chydorids are a potentially important structuring factor within benthic communities (van de Bund & Davids, 1993). For this study, samples were taken from a shallow (*ca* 0.5 m) sand-flat at the exposed North-East side of the lake (Fig. 1).

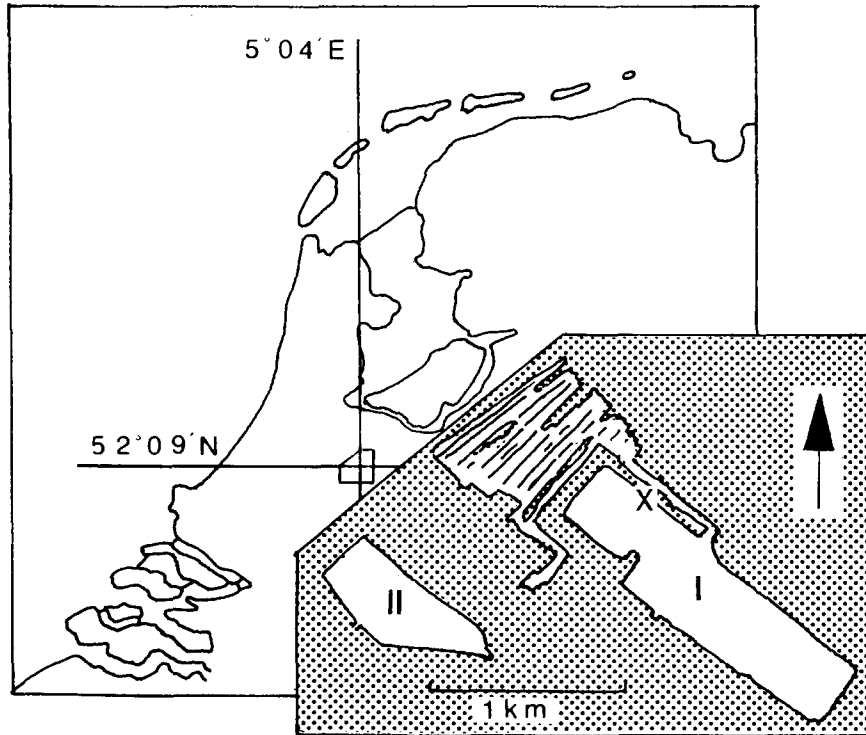


Fig. 1. Map of the Netherlands, showing the location of the lakes Maarsseveen I and II, and the position of the sampling site (X).

Material and methods

Sampling the seasonal variation

From June 1989 until December 1990, samples were taken every fortnight, with the exception of two subsequent sampling dates in September–October 1990, from which no data are available. Samples were taken from a depth of *ca* 0.5 m with a handheld core sampler of 5 cm diameter. At each sampling date, three replicate cores were taken and transported to the laboratory. There, the top 2 cm of each sediment core was removed with *ca* 2 cm of the overlying water, using a specially designed sectioning device. The samples were preserved by adding 0.5 ml 40% formaldehyde.

Samples were processed by centrifugation (4000 rpm, 10 min) in the silica medium Ludox® (De Jonge & Bouwman, 1977; Nichols, 1979); all the organic material, including the macro- and meiobenthic organisms, could thus be collected from the supernatant in an Erlenmeyer flask using a vacuum pump. The remaining silica material was removed from the samples by rinsing them over a 25 µm plankton screen. This method produces very clean samples that

are easily sorted. This centrifugation procedure was repeated once for each sample; recovery of macro- and meiobenthos after two centrifugations was high (>95%).

Macro- and meiobenthic organisms were sorted out, identified and counted under a dissection microscope. Chironomid larvae were identified using the keys of Moller Pillot (1984) and Wiederholm (1983). Head capsule widths of larvae of the most abundant chironomid species were measured to determine larval instar, using the relations between these parameters described in ten Winkel (1987). The key of Flößner (1972) was used for identification of the chydorids.

Oxygen content and temperature of the surface water layer of the lake were measured every fortnight. Data of diatom concentrations in the lake water were taken from the routine sampling programme performed in Lake Maarsseveen I.

Sampling the spatial distribution

To characterise the patterns of distribution of the organisms at different times of the year, additional samples were taken on three occasions: during summer (11 July

1990), and before and after the first large autumn storm of this year (19 and 21 September 1990). The wind direction during this storm was Southwest, with wind velocities up to 18 m s^{-1} measured at the nearby weather station of De Bilt. Storms of this strength occur rather frequently, especially during autumn, causing waves of considerable size and resuspending the fine sediment at the sampling location. During summer, 50 samples were taken in a grid of $2.5 \times 10 \text{ m}$; within this grid, water depth ranged from *ca* 0.4 to 0.7 m. At the other two sampling occasions, 20 randomly located samples were taken, distributed over the same area.

The top 2 cm of the sediment was sampled, using a small hand-held core sampler (surface area 0.79 cm^2). Samples were stained with Rose Bengal and preserved in 4% formalin. Organisms were sorted out and counted under a dissection microscope, using the entire sample; no pre-concentration procedure was applied to avoid any loss of organisms. Chydorid cladocerans and chironomids were identified as described above. Other organisms (as copepods, oligochaetes and ostracods) were counted, but not further identified. Very small organisms as nematodes and rotifers were not taken into account.

The data collected in July were used to characterise the spatial heterogeneity of the organisms at the scale of the sampling grid ($2.5 \times 10 \text{ m}$), using Kruskal-Wallis tests (Sokal & Rohlf, 1981), with the horizontal (parallel to the shore) or vertical position in the grid as independent variables. Spatial correlation between the densities of the taxa at the scale of the sampler (0.79 cm^2) was evaluated by calculating Spearman's coefficient of rank correlation for each pair of taxa.

Spatial heterogeneity was quantified by calculating the Morisita index (I_m ; Morisita, 1971) with its statistic allowing testing for departure from randomness (Elliott, 1977) for the more abundant taxa from the data of all three sampling occasions. This index measures how many times more likely it is that two randomly selected individuals will be from the same sampling unit than it would be if the individuals in the population were distributed at random (Hurlbert, 1990). The Morisita index is independent of the sample mean, but is highly dependent on quadrat size (Elliott, 1977).

Results

Temperature, oxygen and diatom abundance

Water temperature and oxygen content data are presented in Figs 2a and 2b. In 1989, temperatures were higher in the beginning of the summer (averaging $21.0 \text{ }^\circ\text{C}$ from late June to July) than at the end ($19.4 \text{ }^\circ\text{C}$ from August to early September). In 1990, an opposite pattern was observed: water temperatures averaged $19.2 \text{ }^\circ\text{C}$ in the beginning and $21.0 \text{ }^\circ\text{C}$ at the end of the summer, respectively. During winter, water temperatures averaged *ca* $5 \text{ }^\circ\text{C}$. Oxygen concentrations were rather constant throughout the sampling period at *ca* 10 mg l^{-1} ; no notable differences were observed between the two years. The seasonal dynamics of the diatoms are characterised by one major *Melosira* peak in March, and two smaller peaks of *Stephanodiscus* in the summer and fall (June and September in 1989, July and October in 1990).

Occurrence and seasonal pattern of macro- and meiobenthos

The macro- and meiobenthos was largely dominated by chironomid larvae and chydorid cladocerans, respectively. During this study, 18 chydorid species and 19 chironomid taxa were identified (Table 1). In the graphs of the seasonal variation of chironomid and chydorid densities (Figs 3, 4 and 6), the data of the three replicate samples of each date are shown; lines show averaged densities.

Chironomids

Chironomid larval densities were relatively high throughout the sampling period (Fig. 3a), varying from 4200 ind m^{-2} (9 August 1989) to $51\,000 \text{ ind m}^{-2}$ (28 November 1989). Chironomid densities were much higher during autumn and winter than during spring and summer. Most of the 19 chironomid taxa found (Table 1) occurred only occasionally; only *Cladotanytarsus mancus*, *Stictochironomus sticticus*, *Polypedilum* sp., *Tanytarsus* sp. and *Cryptochironomus* sp. were present at high densities ($>100 \text{ ind m}^{-2}$) during the study period or a part of it (Fig. 4). The seasonal variation of these more abundant taxa is described in more detail below, except for *Tanytarsus* sp.. This species reaches its highest density at a depth of *ca* 10 m (Heinis, 1993); at 0.5 m, where we took our samples, densities are relatively low, mak-

Table 1. Chydorid and chironomid taxa found in the littoral of Lake Maarsveen I during the study period (June 1989-January 1991)

Chydoridae

Eurycercinae

Eurycercus lamellatus O.F. Müller

Aloninae

Camptocercus rectirostris Schoedler

Acroperus harpae Baird

Alona guttata Sars

Alona costata Scott

Alona intermedia Sars

Alona rectangula Sars

Alona affinis Leydig

Rhynchotalona falcata Sars

Monospilus dispar Sars

Chydorinae

Disparalona rostrata Koch

Alonella excisa Fischer

Alonella nana Baird

Chydorus gibbus Sars

Chydorus piger Sars

Chydorus sphaericus O.F. Müller

Pseudochydorus globosus Baird

Chironomidae

Tanypodinae

Procladius sp.

Psectrotanytus varius Fabricius

Chironomini

Pseudochironomus sp.

Polypedilum sp.

Endochironomus sp.

Stictochironomus sticticus Fabricius

Glyptotendipes sp.

Cryptotendipes sp.

Harnischia sp.

Cryptochironomus sp.

Demicryptochironomus sp.

Tanytarsini

Cladotanytarsus mancus Walker

Tanytarsus sp.

Orthocladiinae, Diamesinae and Prodiamesinae

Cricotopus sp.

Nanocladius sp.

Parakiefferiella sp.

Prodiamesa sp.

Pseudorthocladius sp.

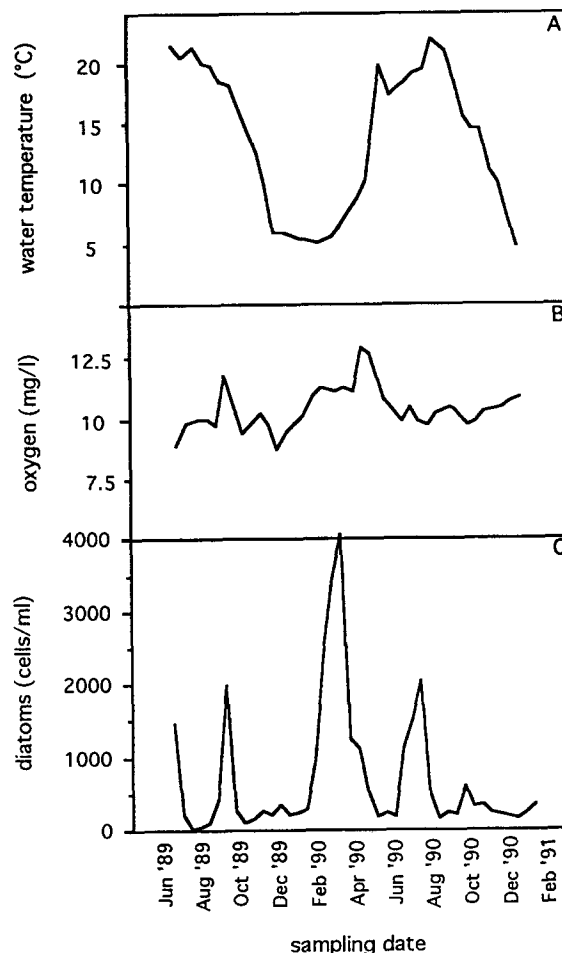


Fig. 2. Seasonal variation of water temperature (A), oxygen content (B) and diatom abundance (C) in the surface 1 meter of the lake.

ing interpretation of these data not very meaningful. Since only the top 2 cm of the sediment was sampled, population densities of chironomid species that burrow deeper are underestimated. This is the case for fourth instar *Stictochironomus sticticus* and – to a lesser extent – *Polypedilum* sp. (ten Winkel, 1987; Heinis, 1993; van de Bund & Groenendijk, in prep.). *Cladotanytarsus mancus*, *Tanytarsus* sp. and *Cryptochironomus* sp. mainly occur in the top 2 cm (ten Winkel, 1987; Heinis, 1993).

Cladotanytarsus mancus. The most abundant chironomid species was identified as *Cladotanytarsus mancus* (Fig. 4a). However, it is not impossible that there were more *Cladotanytarsus* species than only *C. mancus*, as suggested in Heinis & Davids (1993). When sampling adults at different times throughout the study period, however, only *C. mancus* was found. This species

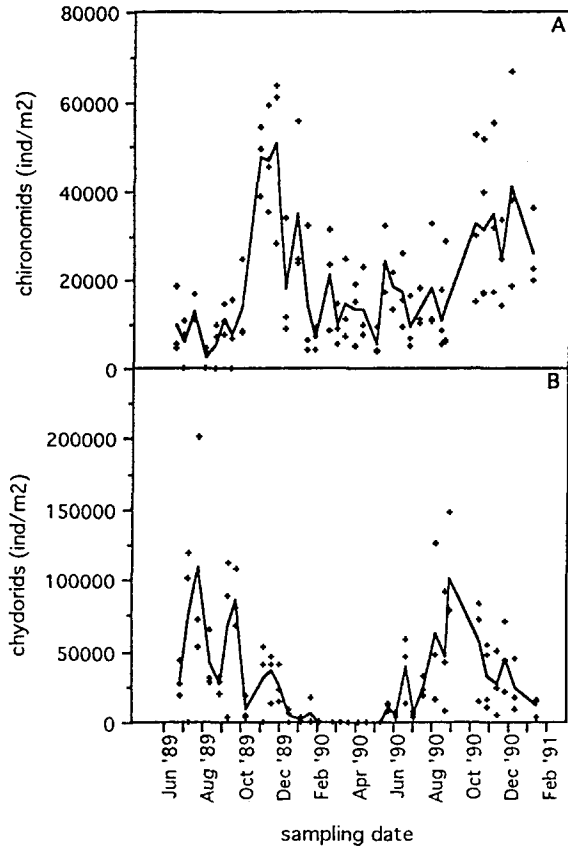


Fig. 3. Seasonal variation of densities of chironomid larvae (A) and chydroid cladocerans (B); lines show averaged densities.

is largely responsible for the high chironomid densities during autumn and winter (Fig. 3a). Densities of this species reached a minimum in summer and early autumn, ranging from 1500 ind m^{-2} (5 July 1990) to $42\,000 \text{ ind m}^{-2}$ (28 November 1989). The instar distribution (Fig. 5a) did not show a clear seasonal pattern, with larvae of all instars present throughout the year. It is noteworthy that even during the winter months, 40–50% of the population of this species had not reached the third instar yet. No obvious recruitment peaks of first-instar larvae could be distinguished, indicating that emergence and settlement in this species do not take place in a synchronised way, but more or less continuously whenever the circumstances are favourable.

Stictochironomus sticticus. Population densities of *Stictochironomus sticticus* (Fig. 4b) were maximally 7400 ind m^{-2} on 31 May 1990. A clear seasonal pattern is visible with high densities in late spring, decreasing slowly during summer and autumn, and remaining low throughout the winter and early spring. *Stic-*

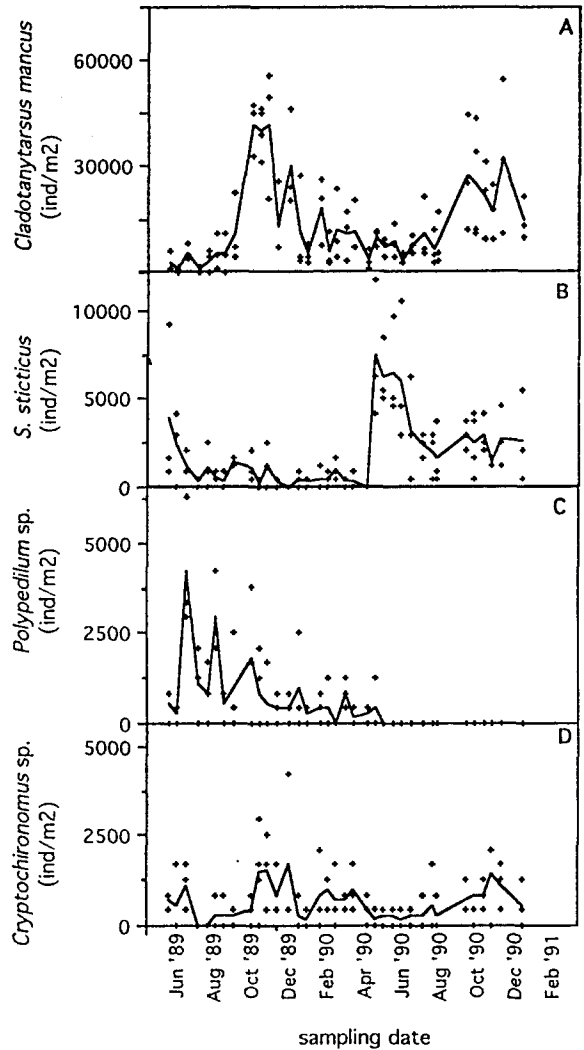


Fig. 4. Seasonal variation of densities of the principal chironomid taxa: *Cladotanytarsus mancus* (A), *Stictochironomus sticticus* (B), *Polypedilum* sp. (C), and *Cryptochironomus* sp. (D); lines show averaged densities.

tochironomus densities were much higher in the season 1990–1991 than in 1989–1990. The instar distribution (Fig. 5b) shows settlement peaks of early instar larvae during the summer and autumn. As mentioned before, the densities of fourth instar larvae are underestimated due to the limited sampling depth. The number of peaks differed between the two years, with several peaks in 1989, and only two in 1990, suggesting flexibility in the number of summer generations. The first settlement peak was by far the most abundant in both years. Throughout the winter, the entire population of

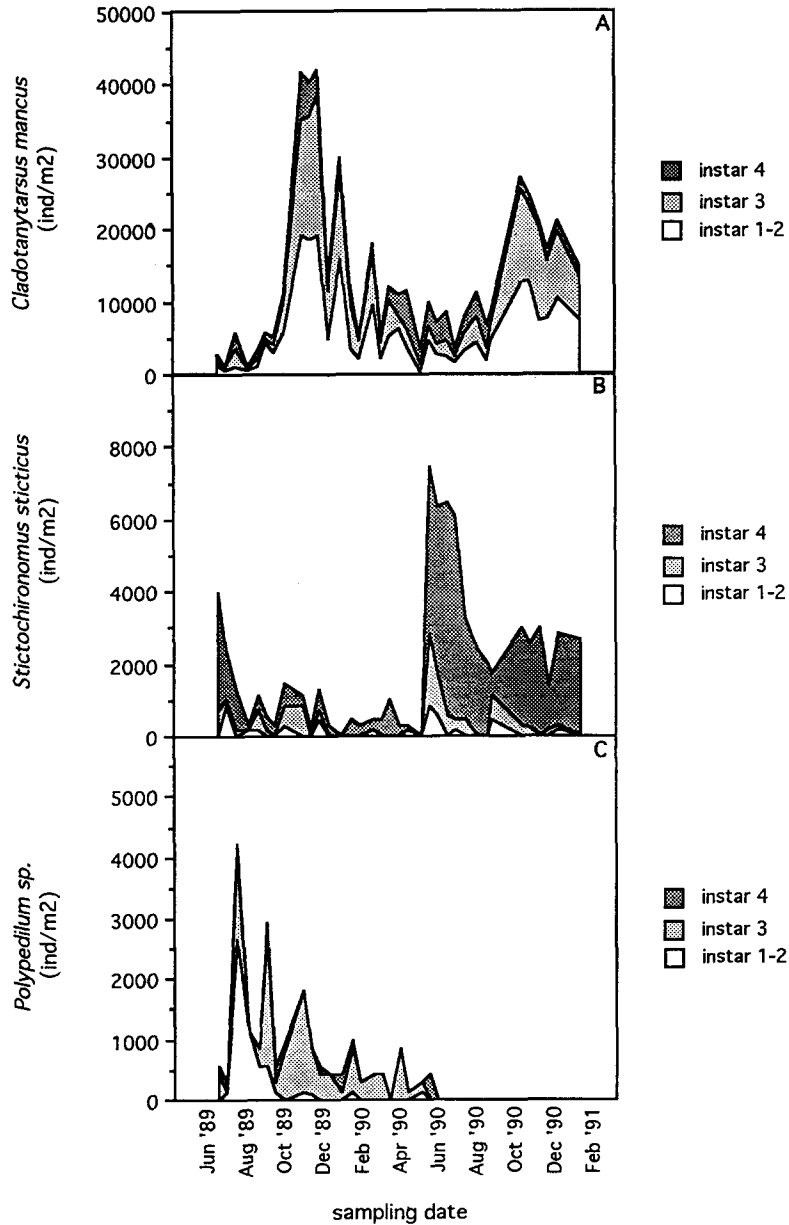


Fig. 5. Cumulative seasonal instar distribution (6-week moving averages) of *Cladotanytarsus mancus* (A), *Stictochironomus sticticus* (B), and *Polypedilum* sp. (C).

this species was in its fourth instar.

Polypedilum sp. Densities of *Polypedilum* sp. (Fig. 4c) were relatively low (maximum 4200 ind m⁻²) until 31 May 1990. After this date, this species had completely disappeared from the sampling site. Just like *Stictochironomus*, early instar larvae of *Polypedilum* settled in several peaks during summer and autumn

(Fig. 5c), with the highest abundance during the first settlement peak.

Cryptochironomus sp. *Cryptochironomus* densities were relatively low (ca 900 ind m⁻²); these larvae were found throughout the sampling period (Fig. 4d). A clear seasonal pattern could not be observed, and there were no differences between the two years.

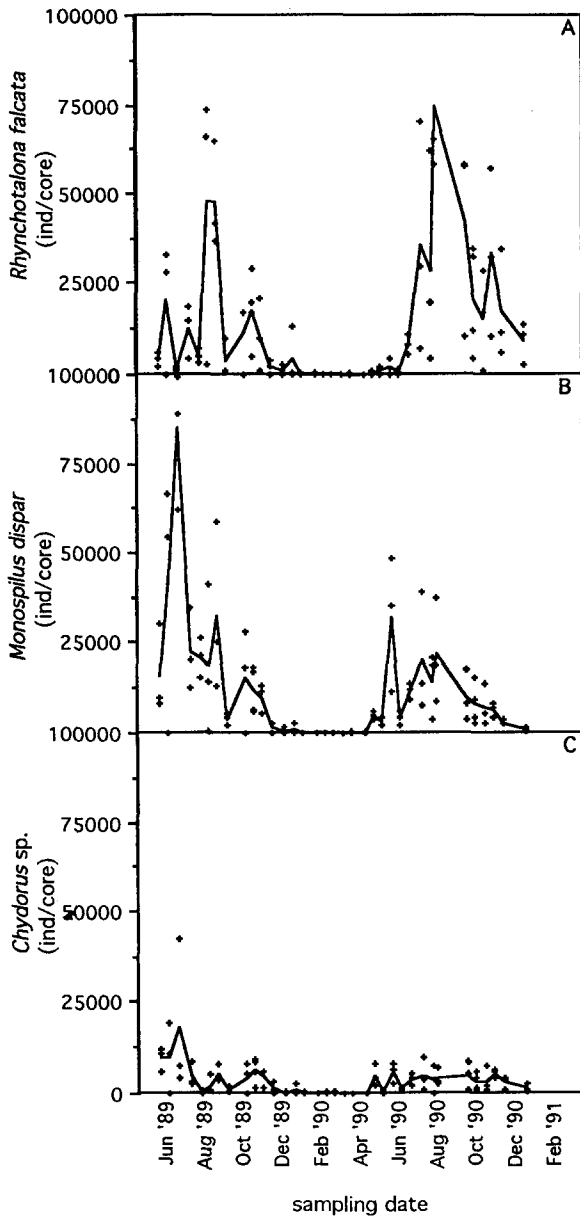


Fig. 6. Seasonal variation of densities of the principal chydorid taxa: *Rhynchotalona falcata* (A), *Monospilus dispar* (B), *Chydorus* spp. (C); lines show averaged densities.

Chydorids

Total chydorid densities showed a very pronounced seasonal variation (Fig. 3b); from January until late May, hardly any chydorids were present, while during summer and autumn densities were extremely high. A maximum density of $110\,300\text{ ind m}^{-2}$ was reached in July, 1989. Although seventeen chydorid species

were found (Table 1), two of them generally constituted >95% of the total chydorid density: *Monospilus dispar* (Fig. 6a) and *Rhynchotalona falcata* (Fig. 6b). The only other chydorid species present in considerable densities were *Chydorus piger* and *Chydorus gibbus* (Fig. 6c). The seasonal variation of these chydorid taxa is discussed below.

Rhynchotalona falcata. This chydorid was found from June to January, with one major density peak in September–October (Fig. 6a). In 1989, the peak density was $47\,700\text{ ind m}^{-2}$ on 21 September, in 1990 $74\,900\text{ ind m}^{-2}$ on 4 September. Except in June–July, *Rhynchotalona falcata* was the most abundant chydorid throughout the summer and the autumn.

Monospilus dispar. *Monospilus dispar* followed a similar seasonal pattern as *Rhynchotalona falcata*, and was also found from June to January (Fig. 6b). This species peaks earlier in the season than *Rhynchotalona*; during its first peak in July, *Monospilus dispar* is the dominating chydorid species. In 1989, the peak density was almost three times as high as in 1990 ($85\,000\text{ ind m}^{-2}$ on 25 July 1989, and $31\,700\text{ ind m}^{-2}$ on 26 June 1990, respectively).

Chydorus spp. Three different *Chydorus* species were found during the sampling period, but *C. piger* and *C. gibbus* were by far the most abundant representatives of this genus. They both followed a very similar seasonal pattern, and densities were comparable. *Chydorus* formed only a minor part of the total chydorid fauna; the highest density that was found during this study was $18\,000\text{ ind m}^{-2}$ (16% of the total chydorid density) on 25 July 1989 (Fig. 6c). The seasonal variation pattern of *Chydorus* was very similar to that of *Rhynchotalona falcata*.

Temporal correlations between taxa

Spearman rank correlation coefficients were calculated from averaged densities of the more abundant taxa discussed above (Table 2). Due to the similarity of their seasonal pattern, highly significant positive correlations were found among the three chydorid taxa *Rhynchotalona falcata*, *Monospilus dispar* and *Chydorus* spp.

Correlation coefficients between chydorids and chironomid taxa were generally non significant, with three exceptions: *Monospilus dispar*, *Chydorus* spp. and

Table 2. Spearman rank correlation matrix between averaged densities of different taxa throughout the sampling period (June 1989 - January 1991; $n = 35$). Significant correlations are indicated: *** - $p < 0.001$, ** - $p < 0.01$, * - $p < 0.05$

	Rhy	Mon	Chy	Cla	Sti	Pol	Cry	Tan	t-chy
Monospilus	0.70***	—							
Chydorus	0.63***	0.82***	—						
Cladotanytarsus	0.16	-0.28	-0.04	—					
Stictochironomus	0.30	0.39*	0.46**	-0.15	—				
Polypedilum	-0.09	0.21	0.06	-0.17	-0.47**	—			
Cryptochironomus	0.01	-0.20	0.07	0.55***	-0.29	-0.04	—		
Tanytarsus	0.26	0.19	0.28	0.48**	0.05	0.13	0.14	—	
tot. chydorids	—	—	—	-0.13	0.37*	0.07	-0.07	0.17	—
tot. chironomids	0.22	-0.13	0.14	—	—	—	—	—	-0.01

total chydorid densities were significantly positive correlated with *Stictochironomus sticticus*.

Densities of the chironomid *Cladotanytarsus mancus* were significantly positive correlated with *Cryptochironomus* sp. and *Tanytarsus* sp., respectively. The only significant negative correlation found in this study was between *Stictochironomus sticticus* and *Polypedilum* sp. densities. During the season 1989–1990, both species were present in comparable densities with several settlement peaks during summer and autumn; furthermore, the peaks of the two species seem to alternate (Fig. 5). In the spring of 1990, there was a relatively high *Stictochironomus* settlement, coinciding with complete disappearance of *Polypedilum*.

Spatial heterogeneity

The densities of the most important taxa at the three sampling occasions are presented in Table 3. Generally, the density estimates correspond reasonably well with those obtained in the seasonal sampling with larger cores (Figs 3, 4 and 6). Ostracods and copepods were present with maximum densities of 14 400 ind m⁻² and 16 900 ind m⁻², respectively; ostracod densities were highest in summer, copepod densities in autumn. Generally, the variances exceeded the means by far, indicating that the distributions were highly heterogeneous.

Densities were affected by the autumn storm, but only in the cases of *Rhynchotalona falcata* and total chydorid density, the effect was significant (Mann-Whitney U-test, $p < 0.05$). Densities of these taxa were lower after the storm than before.

Table 3. Averaged densities with variances of the principal taxa at three sampling dates for spatial heterogeneity. Only taxa with density > 6000 ind m⁻² at any of the sampling dates are included.

	11 July $n = 49$	19 September $n = 20$	21 September $n = 20$
10 ⁴ ind m ² (variance)			
<i>Cladotanytarsus mancus</i>	1.35 (2.69)	1.09 (1.86)	1.30 (1.52)
total Chironomidae	1.98 (3.30)	1.77 (2.44)	1.66 (1.91)
<i>Monospilus dispar</i>	3.84 (25.80)	2.52 (5.66)	1.82 (6.00)
<i>Chydorus piger</i>	0.92 (1.43)	0.45 (0.52)	0.24 (0.26)
<i>Rhynchotalona falcata</i>	0.46 (0.68)	8.77 (23.59)	6.32 (36.51)
total Chydoridae	5.45 (35.84)	11.74 (30.87)	8.45 (58.83)
Ostracoda	1.44 (3.02)	0.38 (0.28)	0.47 (0.45)
Copepoda	0.62 (0.75)	1.69 (4.36)	1.15 (1.20)

Using the data from the summer sampling, no significant relation could be established between densities of any of the organisms and either the length or the depth coordinates of the grid (Kruskall-Wallis test, $p > 0.05$; Table 4). Therefore, it was concluded that the sampling area can be considered homogeneous with respect to the distribution of these organisms, and random samples were taken at the other sampling occasions.

Spatial correlation between taxa

Spearman rank correlation coefficients between the different taxa showed considerable variation (Table 5). *Cladotanytarsus mancus* and total chironomid densities showed no significant correlation with the three meiofauna groups (chydorids, ostracods and cope-

Table 4. Kruskal-Wallis statistics and significance levels of length and depth coordinate of the sampling grid vs. density, using data from 11 July. Only taxa with density $>6000 \text{ ind m}^{-2}$ are included. $n = 49$.

	Length coordinate		Depth coordinate	
	stat.	<i>p</i>	stat.	<i>p</i>
<i>Cladotanytarsus mancus</i>	4.61	0.80	3.62	0.46
total Chironomidae	8.08	0.53	4.30	0.37
<i>Monospilus dispar</i>	9.87	0.36	4.39	0.36
<i>Chydorus piger</i>	14.17	0.11	4.91	0.30
total Chydoridae	11.34	0.25	4.83	0.31
Ostracoda	9.91	0.36	4.58	0.33
Copepoda	10.83	0.29	8.41	0.08

Pods). Higher correlation coefficients were found between the different meiobenthic taxa, with highly significant correlations ($p < 0.01$) between densities of the two chydorid species *Monospilus dispar* and *Chydorus piger*, between *M. dispar* and copepods, and between copepods and ostracods.

Indices of spatial heterogeneity; comparison between the sampling occasions

In July, the Morisita index (Table 6) varied from 1.26 (copepods) to 2.10 (*Monospilus dispar*), in September from 0.47 (ostracods on 19 September) to 2.07 (*Monospilus dispar* on 21 September). In the majority of the cases, this index was larger than one, with distributions that were significantly different from random.

There were considerable differences in the heterogeneity indices as found before and after the autumn storm. For *Cladotanytarsus mancus* and copepods a decreasing spatial heterogeneity was observed following the disturbance. For the chydorids, the effect was opposite: the disturbance resulted in an increasing heterogeneity. Since *Chydorus piger* and ostracod densities were relatively low during autumn ($<5000 \text{ ind m}^{-2}$), no conclusions are drawn from heterogeneity indices found for these organisms.

Discussion

Seasonal variation and life cycles

Population peaks of the dominating macro- and meiobenthic taxa occurred at different times during the two years of this study. In early spring, following the *Melosira* peak and a major temperature increase,

there were settlement peaks of *Stictochironomus sticticus*, in 1989 followed by a *Polypedilum* maximum. In June–July a minor *Stephanodiscus* peak occurred, and the chydorids became dominating constituents of the benthos. A peak of *Monospilus dispar* was followed by a peak of *Rhynchotalona falcata*. In autumn, after the second *Stephanodiscus* peak, the chironomid *Cladotanytarsus mancus* became the dominant species, remaining so throughout the winter.

The seasonal dynamics of the chironomid larvae are mostly similar to those reported in previous studies (Ten Winkel & Davids, 1987a; Heinis, 1993). The picture that emerges is that *Cladotanytarsus mancus* in this lake has a polyvoltine population which emerges throughout the spring and autumn; this is consistent with the finding of imagines from the second half of June until at least mid September (Kouwets & Davids, 1984). However, at least in some years major emergence peaks can occur (Heinis, 1993). *Stictochironomus sticticus* and *Polypedilum* sp. are mono- to bivoltine species with a major emergence peak and consecutive settlement in early spring, and eventually a minor peak during summer. An advantage of settlement in early spring can be that at that time the chydorid populations have not yet built up, and interactions with chydorids will thus be avoided. In laboratory experiments it was shown that chydorid populations can have a negative effect on the growth and development of early instar chironomid larvae (van de Bund & Davids, 1993), so early settlement can certainly be advantageous.

The *Stictochironomus sticticus* population in Lake Maarsseveen I is heavily predated upon by bream and water mites; effects of bream on chironomid densities were shown directly in enclosure experiments (ten Winkel, 1987). This author found that during autumn the impact of bream predation was very significant, accounting for most of the decline in the population. During summer, no effect of bream was observed on the *Stictochironomus* population; then predation by water mites is considered as the main cause of mortality.

The two dominating chydorid species, *Monospilus dispar* and *Rhynchotalona falcata*, are typical inhabitants of sandy sediments (Goulden, 1971; Flößner, 1972; Smirnov, 1974; Chengalath, 1982), and are classified as detritivores (Flößner, 1972). Visual observation of the behaviour of these two species in the sand shows that *Monospilus dispar* crawls freely through the sand, sometimes burrowing some millimetres below the surface, while *Rhynchotalona falcata* always keeps itself

Table 5. Spearman rank correlation coefficients of densities of all pairs of taxa, using the data from 11 July; $n=49$. Only taxa with density $>6000 \text{ ind m}^{-2}$ are included. Significant correlations are indicated: ** - $p < 0.01$; * - $p < 0.05$.

	<i>C.m.</i>	tot. Chir.	<i>M.d.</i>	<i>C.p.</i>	tot. Chyd.	Ostr.
<i>M. dispar</i>	0.10	0.17				
<i>C. piger</i>	0.08	-0.02	0.50 (**)			
tot. Chydor.	0.08	0.10				
Ostracoda	0.00	0.03	0.24	0.20	0.32 (*)	
Copepoda	0.09	0.12	0.39 (**)	0.08	0.35 (*)	0.47 (**)

Table 6. Morisita heterogeneity index of the principal taxa at three sampling dates. Significant departures from randomness ($I_d = 1$) are indicated: ** - $p < 0.01$; * - $p < 0.05$. Only taxa with density $>6000 \text{ ind m}^{-2}$ at any of the sampling dates are included.

Morisita index of heterogeneity I_d	11 July $n=49$	19 September $n=20$	21 September $n=20$
<i>Cladotanytarsus mancus</i>	1.57 (**)	1.50 (*)	1.15
total Chironomidae	1.23 (**)	1.17	1.12
<i>Monospilus dispar</i>	2.10 (**)	1.39 (**)	2.07 (**)
<i>Chydorus piger</i>	1.44 (**)	1.27	1.40
<i>Rhynchotalona falcata</i>	1.81 (**)	1.15 (**)	1.65 (**)
total Chydoridae	1.73 (**)	1.10 (**)	1.61 (**)
Ostracoda	1.54 (**)	0.47	0.95
Copepoda	1.26	1.72 (**)	1.09

firmly attached to detritus particles at the sediment-water interface. Our finding that *Monospilus dispar* peaks earlier in the year than *Rhynchotalona falcata* may be related to this difference in habitat utilisation; early in the season there may be not enough accumulated detritus for *Rhynchotalona falcata* to serve as a substrate, and sedimented diatoms of the first *Stephanodiscus* peak may provide this. In contrast with the results of a preliminary survey in lake Maarsveen I (Davids *et al.*, 1987), *Disparalona rostrata* was not found to be an important constituent of the chydorid fauna in this study. However, the former survey was only based on one single sampling occasion.

In some studies (Goulden, 1971; Robertson, 1990) the summer decrease of chydorid populations is attributed to predation by carnivorous chironomids. In the littoral of lake Maarsveen I, however, hardly any predatory chironomids are found. Water mite species as *Arrenurus crassicaudatus* and *Mideopsis orbicularis* are found in considerable numbers at this depth

(Davids *et al.*, 1994), and are likely to predate on chydorids (Davids, personal communication). It remains unclear whether these predators can be responsible for the observed decrease; it is also possible that other factors, as food availability or intra- and interspecific competition, regulate population densities of the littoral chydorids in this lake.

Spatial heterogeneity and its short-term variability

A very small size core (surface area 0.79 cm^2) sampling the top 2 cm of the sediment, was used in this study. This was aimed to collect information on the spatial distribution of the meiobenthos: chydorids, ostracods and copepods. These organisms are mostly limited to the sediment surface and the top 1 cm of the sand. Using a core of this size, the more abundant taxa were sampled at densities of *ca* $5-10 \text{ ind core}^{-1}$; this is sufficient for a meaningful statistical interpretation of the data. However, densities of macrobenthic organisms

are lower (<2 ind core⁻¹); consequently, interpretation of the data for these organisms is more difficult.

This study clearly shows that the spatial distribution of the meiobenthos is highly heterogeneous. This is consistent with the findings of numerous other studies (e.g. Whiteside *et al.*, 1978; Gilinsky, 1984; Meire *et al.*, 1989). This implies that individual organisms experience conditions that differ considerably from what one would conclude from averaged data.

Furthermore, the degree of heterogeneity did vary in a period of only two days (Table 6). Most likely, this is caused by the storm that occurred within this period, but we can not be certain about that since we have no information on changes in heterogeneity on this time-scale in absence of disturbance. Whatever the cause, since the Morisita index quantifies encounter rates between individual organisms (Hurlbert, 1990), short-term changes of this index as found in this study have direct relevance for density-dependent processes as competition and predation.

Densities also changed in the two days between the autumn samplings (Table 3); *Cladotanytarsus mancus* and ostracod densities were slightly higher after the storm than before, but this difference was not significant. Chydorid densities, however, decreased significantly with *ca* 30%. This is most likely caused by transport of organisms to less exposed areas. The chydorid species involved are closely associated with detritus particles (Flößner, 1972), and the several large storms occurring each year are thought to be responsible for the redistribution of this fine material in lake sediments (Rowan *et al.*, 1992). Wind-induced wave action causes detrital material to accumulate in patches (Beattie, 1982); the decrease in density and the increase in spatial heterogeneity of the chydorids following such a storm as found in this study could be explained by the transport of these organisms together with the detritus they are associated with.

Temporal and spatial correlations

Both temporal (Table 2) and spatial (Table 5) correlations between macro- and meiobenthic taxa were mostly weak, suggesting that there are no strong interactions between these groups, and that their distribution patterns are independent of each other. Among the meiofaunal taxa, however, significant positive spatial and temporal correlation coefficients were found; apparently, the similarity in both seasonal dynamics and spatial distribution is larger among the meiofaunal taxa than between macro- and meiofaunal taxa. Among the

chironomid species, significant positive temporal correlations were found between *Cladotanytarsus mancus* and both *Cryptochironomus* and *Tanytarsus*; these three species have similar seasonal dynamics, with highest densities found in the autumn. Between two other chironomid taxa, i.e. *Stictochironomus sticticus* and *Polypedilum* sp., a significant negative correlation was found, in spite of similarities in the life histories of these species; they are both uni- to bivoltine with a major settlement peak in early spring. Visual observation of *Stictochironomus sticticus* and *Polypedilum* sp. in the laboratory revealed that these species had a very similar feeding behaviour and tube structure, suggesting that they rely on similar food resources. However, no data of gut contents of the two species are available to confirm these observations. These species are temporally separated: *Stictochironomus* settles first, *ca* 2 weeks thereafter followed by *Polypedilum*. This may be caused by differences in synchronisation patterns of the development during winter; *Stictochironomus* populations in Lake Maarsseveen synchronise during winter by means of a diapause (Kikkert, personal communication), probably enabling them to emerge synchronously so early in spring. By settling two weeks later, *Polypedilum* will avoid interference with early instar *Stictochironomus* larvae; by then, these are already in instar 3–4, and have burrowed deeper into the sediment (Olafsson, 1992; van de Bund & Groenendijk, *in prep.*). The failure of *Polypedilum* to settle in 1990 following the pronounced *Stictochironomus* peak may be caused by interference between these two species; an alternative hypothesis is that emergence of *Polypedilum* failed that year. The picture that emerges for these two species is that their life cycles are complementary, enabling them to occur together in very similar niches, with *Polypedilum* making use of 'gaps' in the life cycle of *Stictochironomus*.

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