Dynamics of metal adaptation in riverine chironomids.
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CHAPTER II

Seasonal dynamics and larval drift of *Chironomus riparius* (Diptera) in a metal contaminated lowland river

ABSTRACT

*Chironomus riparius* is one of the insect species which inhabit polluted rivers in large densities, indicating a high adaptive capacity. Previous studies showed that this capacity is expressed by the occurrence of adapted strains in metal-polluted rivers. Differences in life history between metal exposed and non-exposed midges have been demonstrated in laboratory experiments, and therefore a comparative field study of seasonal dynamics was carried out at two metal-polluted sites and one reference site. Just downstream from a massive metal discharge, seasonal dynamics were almost identical to the upstream reference site. Circa four generations per year were produced. Further downstream, lower larval densities were recorded, especially during the second half of the sampling period. The influx of upstream *C. riparius* larvae into polluted sites was estimated by measuring larval drift just upstream from the point source of metal contamination and indicated a massive input to the standing stock downstream. It is concluded that drift of non-tolerant larvae is dominating the seasonal dynamics of midges downstream. Accordingly, genetic uniformity of chironomids inhabiting upstream and downstream sites is expected most of the time. However, research performed during the last decade, demonstrated that genetically adapted strains of *C. riparius* may develop at certain stages in the seasonal cycle. However, a stable metal-adapted *C. riparius* population at the first downstream site, is most likely present on rare occasions only.
CHAPTER II

Introduction

Chironomus riparius Meigen, 1804 is one of the invertebrate species inhabiting lowland rivers in Belgium and the southern part of the Netherlands. One of these rivers, the River Dommel, is strongly polluted with metals from a distinct point source in the river. Dissolved cadmium and zinc concentrations in the Dommel, downstream from the polluter, regularly exceed substantially chronic No Observed Effect Concentrations (NOEC) for growth, reproduction and mortality of C. riparius (Postma et al 1994; Timmermans et al 1992). Nevertheless, flourishing midge populations are found at metal contaminated as well as reference sites in the river. This apparent contradictory observation has been explained by the adaptive capability of this midge species as found in metal-exposed laboratory cultures (Postma & Davids 1995; Miller & Hendricks 1996). These findings were corroborated in the metal-polluted River Dommel, because midges sampled at exposed sites have shown to be less sensitive to cadmium compared to unexposed chironomids (Postma et al 1995a; 1995b). By the standards set in Brandon (1990) to review a genetic component in adaptation to toxicants, the adaptation to metals in the River Dommel was judged to be genuinely genetic (Postma & Groenendijk 1999). However, additional differences in life history characteristics have been recorded between metal-exposed midges from different sites in the river. Midges (F1) originating from the metal-polluted sites were characterised by either a high control mortality or an increased larval development time (Postma et al 1995a). These differences imply that in situ seasonal dynamics show location specific differences.

Metal adaptation in arthropods has been extensively studied in stable habitats like soils (Posthuma & van Straalen 1993) or in a confined experimental set-up (Postma et al 1995a; 1995b). It has not been shown, however, how metal adapted and non-adapted invertebrates interact in the highly dynamic regime of a river. It may be that separate subpopulations are maintained by reproductive isolation, like in Chironomus plumosus populations in a freshwater lake in Denmark. Pedersen (1988) showed that
seasonal differences in the emergence patterns between shallow and deeper lake areas considerably limited the gene flow between two *C. plumosus* populations. He proposed that this was the main reason for the maintenance of two separate Mendelian populations within the same lake.

The present study aimed to investigate the seasonal dynamics of larval density of *C. riparius*, inhabiting both metal exposed and non-exposed sites in the contaminated lowland river Dommel by comparing instar composition and frequency distributions at three different stations. In conjunction, the number of non-exposed larvae drifting into metal-exposed sites further downstream was measured. These observations, together with the results of ongoing studies on the interbreeding of chironomids inhabiting sites differing in metal exposure, will elucidate the possibility of reproductive isolation of metal-adapted *C. riparius* chironomids in the River Dommel.

**Materials and Methods**

**study sites**

Research was conducted in the River Dommel, a tributary of the River Meuse (figure 2.1). The Dommel, which is a typical lowland river fed by rainwater, is characterised by a sandy bottom, a width of 5-7 m, a depth of 0.4-1.5 m, a current velocity varying between 0.3 and 0.8 m s\(^{-1}\) and neutral waters with a naturally high iron content. The visibility is often limited to 10-20 cm due to suspended organic material, but seasonal variation does occur. The Dommel rises in the northern part of Belgium and a small stream, the Eindergatloop, enters the river at the Dutch border (figure 2.1). On the banks of the Eindergatloop a zinc factory of Union Minière is situated, which has been in production since 1888. Although background levels of some metals (for example, zinc and iron) in the Dommel are already elevated upstream from the confluence with the Eindergatloop, cadmium contamination originates largely from this point source (Postma 1995).
Three sampling sites were selected in the Dommel: 1) a reference location situated about 100 metres upstream from the Eindergatloop (abbreviated as DEG), 2) the first polluted location Neerpelt (NP) about 500 metres downstream from the zinc factory and 3) the second polluted site Borkel (B) located circa seven kilometres downstream from the Eindergatloop (figure 2.1).

![River Dommel and sampling sites](image)

**FIGURE 2.1:** Location of the sampling sites. The River Dommel is indicated in detailed inset.

**field sampling of *Chironomus riparius***

Chironomids were sampled from January 1995 to January 1996 close to the river bank where organic material settles. Water temperature was measured in the middle of the stream at a depth of approximately 10 cm. Monthly sampling took place during winter, while from February to October samples were taken every fortnight. Study sites were visited in random order on every sampling occasion. Eight replicate samples of the benthic fauna were taken at each location using a hand-held corer (surface area 22.9 cm$^2$). Samples were transported to the laboratory and kept at 4 °C prior to sorting.
All samples were processed within 24 hours after sampling. In order to separate chironomid larvae from sediment particles, samples were first sieved using a 150 μm sieve. Samples were then processed by flotation in an oversaturated salt solution (Anderson 1959). The organic fraction, including the benthic organisms, was collected using a vacuum pump. This flotation technique was used because many first and second instar larvae are easily overlooked when sorting untreated samples (Carter 1976). Samples were preserved and stored in circa 4% formaldehyde before identification took place.

Chironomid larvae were identified to family level using the key of Moller Pillot (1984). Larvae of the genus *Chironomus* were identified to genus level based on the presence of ventral tubuli. It was shown by Postma (1995), that based on karyotypic identification, probably all *Chironomus* larvae in the Dommel belong to *C. riparius*. Control identification of emerged male imagoes using the key of Pinder (1978), confirmed that in the present study *Chironomus* larvae from the Dommel also belonged to *C. riparius*. The different larval stages were determined by measuring the width of larval head capsules using the known relationship between these parameters for *C. riparius* (unpublished data). Although it is difficult to identify first instar chironomid larvae to species level, the first instar larvae presented here can safely be assumed to be larvae of *C. riparius*, because peaks of these first instar larvae were normally followed by peaks of unequivocally identifiable second instar larvae. Furthermore, these first instar larvae were compared to first instar larvae from a laboratory culture, of which larvae have been cytologically determined to be *C. riparius* (Postma 1995). Criteria developed by these direct comparisons under a light microscope (600 times magnification) were: 1) the presence of a central medial tooth at the mentum, 2) the shape of the antennae characteristic for larvae of the tribe Chironomini and 3) the presence of two separated ocelli. Only larvae which satisfied the above mentioned criteria were identified as first instar *C. riparius* larvae.
drift measurements

Larval drift was measured at the reference site DEG at the same time as the core samples were taken. A 250 μm net (30 cm wide) was held in the middle of the river just under the water surface for three successive 4-8 minute periods. Stream velocity (current meter: A.OTT Kempen), depth and width of the river were measured simultaneously to calculate water discharge at this sampling site. The filtered water volume varied between 5.7 and 16.3 m$^3$. All drift measurements were carried out between 10:00 AM and 1:00 PM, and each collected drift sample received a similar treatment as the core samples. Only the numbers of intact chironomid larvae and pupae were counted.

water and detritus characteristics

Water samples were collected from the middle of the stream using acid-washed polyethylene bottles at a depth of approximately 10 cm. These water samples were centrifuged for five minutes at 3000 r min$^{-1}$ and acidified thereafter. Samples of the top sediment layer were collected in acid-washed polyethylene bottles and were stored (frozen) prior to preparation. These samples, containing a mixture of sediment and organic material, were sieved using a mesh size of 0.6 mm. Thereafter, sand and other heavy particles were allowed to settle during 60 s. This procedure was repeated twice. The resulting suspension was carefully suctioned off after standing overnight. The particles sedimenting out of this suspension were collected and stored (freeze-dried) for later analyses. This procedure increased the amount of organic carbon in the samples to circa 35% (table 2.1). This material will hereafter be referred to as detritus which is widely used as food by chironomids (Rasmussen 1984a). Concentrations of metals in detritus will therefore, characterise the exposure of the different chironomid larvae better than metal concentrations in total sediment, although metal concentrations in detritus will be affected by this preparation method. Detritus samples were digested in HNO$_3$ (Baker Ultrex) using a microwave equipped with a temperature and pressure control programme. Water and detritus samples were analysed (n = 2-4) with Graphite Furnace Atomic
Absorption Spectrometry (Perkin Elmer 5100) equipped with Zeeman background correction, or air-acetylene Flame Atomic Absorption Spectrometry (Perkin Elmer 1100B). Quality control of metal analyses was carried out by analysing destruction blanks and reference material (NIST: 2704 Buffalo River Sediment). Measured values agreed with certified values (less than 10% deviation) and destruction blanks were near detection limits. Principal water and detritus characteristics for each location can be found in table 2.1 & figure 2.2.

Table 2.1: Average values (n = 21-23) ± standard error of principal water and detritus (based on dry weight) characteristics from the different field sites recorded between January 1995 and January 1996. For seasonal variation of some of the characteristics see also figure 2.2.

<table>
<thead>
<tr>
<th>Location</th>
<th>DEG</th>
<th>Neerpelt</th>
<th>Borkel</th>
</tr>
</thead>
<tbody>
<tr>
<td>distance (m) from point source of metal pollution</td>
<td>-100</td>
<td>+500</td>
<td>+7000</td>
</tr>
<tr>
<td>parameter units</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dissolved metals</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cd</td>
<td>nM</td>
<td>5.1 ± 0.6</td>
<td>638 ± 101</td>
</tr>
<tr>
<td>Zn</td>
<td>µM</td>
<td>2.0 ± 0.2</td>
<td>14.7 ± 1.1</td>
</tr>
<tr>
<td>Cu</td>
<td>nM</td>
<td>59.6 ± 6.4</td>
<td>119.3 ± 11.9</td>
</tr>
<tr>
<td>Fe</td>
<td>µM</td>
<td>5.8 ± 0.6</td>
<td>4.2 ± 0.8</td>
</tr>
<tr>
<td>Mn</td>
<td>µM</td>
<td>1.1 ± 0.1</td>
<td>2.7 ± 0.2</td>
</tr>
<tr>
<td>Detritus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>loss on ignition%</td>
<td></td>
<td>33.5 ± 0.5</td>
<td>38.9 ± 0.6</td>
</tr>
<tr>
<td>Cd</td>
<td>mmol kg⁻¹</td>
<td>0.24 ± 0.02</td>
<td>3.5 ± 0.5</td>
</tr>
<tr>
<td>Zn</td>
<td>mmol kg⁻¹</td>
<td>40.8 ± 2.6</td>
<td>85.4 ± 6.1</td>
</tr>
<tr>
<td>Cu</td>
<td>mmol kg⁻¹</td>
<td>3.3 ± 0.1</td>
<td>6.0 ± 0.3</td>
</tr>
<tr>
<td>Fe</td>
<td>mol kg⁻¹</td>
<td>1.21 ± 0.06</td>
<td>0.93 ± 0.05</td>
</tr>
<tr>
<td>Mn</td>
<td>mmol kg⁻¹</td>
<td>8.7 ± 0.6</td>
<td>2.9 ± 0.2</td>
</tr>
</tbody>
</table>

Differences in larval density among locations were statistically analysed using one-way ANOVA according to Sokal & Rohlf (1981). When assumptions for ANOVA were violated, non parametric Kruskal-Wallis (KW) tests were performed. Five percent significance level was used for rejection of $H_0$ in all cases.
Results

water and detritus characteristics

The seasonal variation in temperature at the three sampling sites is shown in figure 2.2A. Water temperatures increased during the year from 6 °C in January to a maximum of nearly 20 °C in July. No significant differences existed between sampling sites (ANOVA: $F = 0.12; p = 0.89$). Water discharge (figure 2.2B) of the Dommel at the reference site DEG was stable from May 1995 until January 1996 (circa 1.0 m$^3$ s$^{-1}$), but peaked in February 1995 to almost 5.0 m$^3$ s$^{-1}$, when north-western Europe was under the influence of heavy rainfall. Dissolved Cd (figure 2.2C) and Zn (figure 2.2D) concentrations differed significantly among sampling sites (KW = 45.9 and 45.0 respectively; $p < 0.001$). Concentrations of Cd (figure 2.2E) and Zn (figure 2.2F) in detritus also differed significantly among locations (KW = 46.8 and 32.9 respectively; $p < 0.001$). Cd and Zn concentrations in both water and detritus were much higher downstream from the outlet of the zinc factory. However, only small differences in concentrations were found between the two polluted sites. At Neerpelt, the first polluted location, dissolved concentrations of both Cd and Zn were slightly higher compared to those at Borkel, which is located further downstream (figure 2.2C & 2.2D). This is also indicated by the average values (table 2.1). Metal concentrations in detritus were on average higher at Borkel, the second polluted location (table 2.1).

seasonal dynamics of Chironomus riparius

*Chironomus riparius* was generally the most abundant chironomid species present at all sampling sites. Proportions of *C. riparius* expressed as percentages of total chironomids varied between 0%, when for instance emergence of *C. riparius* took place, and more than 86% during summer. Other chironomid subfamilies and species found included *Prodiamesa olivacea* (Meigen, 1818) and various Orthocladiinae, Tanypodinae and Tanytarsinii.
FIGURE 2.2: Seasonal variation of (A) water temperature (°C), (B) water discharge (m³ s⁻¹), (C) dissolved Cd concentrations (nM), (D) dissolved Zn concentrations (µM), (E) Cd concentrations in detritus (mmol kg DW⁻¹) and (F) Zn concentrations in detritus (mmol kg DW⁻¹) at the three sampling locations • = DEG; ○ = Neerpelt; ■ = Borkel) during January 1995-January 1996.

The total densities of *C. riparius* larvae throughout the year are shown for each location in figure 2.3. In winter densities were low, circa 2000 individuals m⁻², except at Borkel where densities exceeded 16,000 individuals m⁻². During spring and summer maximum densities of 20,000 at Borkel to more than 70,000 individuals m⁻² at Neerpelt in November were observed. Densities at the three locations were similar until late July, but from August onwards densities at Borkel dropped to less than 1000 individuals m⁻².
FIGURE 2.3: Seasonal dynamics of total densities of *Chironomus riparius* larvae at the three sampling locations. Mean values with standard errors are shown.
FIGURE 2.4: Seasonal dynamics of the four larval instars of *Chironomus riparius* at the reference location DEG, the first polluted location Neerpelt and the second polluted location Borkel. Plus signs in the graph of the fourth instar larvae indicate the presence of pupae in the sediment. Mean values with standard errors are shown.
The seasonal variation in numbers of the different instars of *C. riparius* at the reference location DEG is shown in figure 2.4. At the start of the sampling period, the winter cohort consisted mainly of fourth instar larvae. Only 10% of *C. riparius* wintered as third instar larvae. Emergence took place in March, as indicated by the presence of pupae and decreasing fourth instar densities. During the second half of April, first instar larvae settled in low densities followed by a peak of second instar larvae in the beginning of May. While third instar larvae could not be traced, fourth instar larvae and pupae of most probably this cohort were found on the last sampling date in May. After this first spring cohort, settlement of first instar larvae occurred at least four times more, resulting in consecutive peaks with increasing densities of all other instars during summer, indicating a multivoltine life cycle with circa four generations in 1995. However, judging the width of the peaks during summer and the presence of pupae from July until September, clear separation of different generations is extremely difficult. The large standard errors on October 24 are due to one exceptional core sample containing many more first and second instar larvae than all other samples. Calculated densities without this sample are for first instars 5740 individuals m$^{-2}$ (SE: 992) and for second instar larvae 3806 individuals m$^{-2}$ (SE: 1034), still presenting peaks of these younger instars. Additionally, larval densities decreased in November and December to circa 2000 individuals m$^{-2}$, mainly third and fourth instar larvae. This indicates winter mortality or drift, resulting in lower densities compared with those at the start of the sampling period in January 1995.

At the first polluted site Neerpelt, settling of first instars throughout the year and densities of the different larval instars showed a pattern similar to the seasonal dynamics at the reference location DEG (figure 2.4). No significant differences in total larval densities (KW = 0.051; p = 0.82) or in the densities of the four separate larval instars (ANOVA (instar 2; F = 1.06) and KW (instar 1, 3 and 4; 0.033 < KW < 0.12); 0.30 < p < 0.86) could be detected between the reference site and the first polluted site.

At the second polluted location Borkel (figure 2.4), seasonal dynamics of larval densities were comparable to the reference location DEG only until
the end of July. In August, however, densities dropped to less than 1000 individuals m$^{-2}$. During the second half of 1995 densities of larval instars in any stage never exceeded 1500 individuals m$^{-2}$, resulting in significant differences in total larval density (KW = 13.17; p < 0.001) and in the densities of the four separate larval instars ($9.30 < KW < 14.56; p < 0.01$ (instar 1), $p < 0.001$ (instar 2-4)). This is in sharp contrast with the high densities of *C. riparius* observed during the second half of 1995 at the reference site DEG and the first polluted location Neerpelt.

**drift**

The number of drifting larvae expressed as total number of all larval instars per m$^3$ river water, was measured at the reference location DEG just before the zinc factory (figure 2.5A). All drifting larvae measured at this location originate from non-exposed locations and would, after passing the point source of metal pollution, directly enter metal-exposed sites. These measurements showed a distinct transport of non-exposed larvae towards the polluted site Neerpelt during July to September and minor peaks during winter. Only low numbers were measured during March to June. The number of drifting larvae, calculated as total numbers of all instars of *C. riparius* larvae per hour, is shown in figure 2.5B. These calculated numbers demonstrate roughly a similar pattern, indicating that larval drift correlated with water discharge in the river. However, the high number of larvae in February 1995 was caused by high water discharge of the River Dommel. In February water discharge was 4.9 m$^3$ s$^{-1}$ at DEG (figure 2.2B), more than three times the average value of 1.4 m$^3$ s$^{-1}$. In summer the high number of drifting larvae coincided with high larval densities at upstream locations (cf figure 2.3). During winter, most of the *C. riparius* larvae found in the drift samples were fourth instars. From May until September 1995 the proportion of fourth instar larvae fluctuated around 30%, while the proportion of third instar larvae varied between 50-60%. During summer, low numbers of first and second instar larvae were also present in the drift samples. It should be noted however, that due to the used mesh size of the drift net (250 μm), most likely large numbers of first and second instar larvae
have passed the net. Pupae were found in small numbers during the emergence peak in early spring and during August and September (figure 2.5A & 2.5B).

FIGURE 2.5: Seasonal dynamics of drifting *Chironomus riparius* larvae (open symbols) and pupae (black symbols) at the reference location DEG. Mean values with standard errors are shown. Figure A shows the number of drifting individuals m\(^{-3}\), figure B shows an estimation of drifting individuals hr\(^{-1}\) (*1000).

**Discussion**

**differences in seasonal dynamics**

The presented data illustrated that *C. riparius* in the River Dommel is a multivoltine species which produced circa four generations during 1995. At temperate latitudes, multivoltine life-cycles are normal for *C. riparius* (Gower & Buckland 1978; Learner & Edwards 1966). Maximum densities of
C. riparius varying between 5000 and 23,000 larvae m\(^2\) have been observed by Davies & Hawkes (1981) and Learner & Edwards (1966). However, under favourable conditions, C. riparius can reach densities between 40,000 and 50,000 individuals m\(^2\) (Köhn & Frank 1980; Rasmussen 1984b). *Chironomus riparius* is further known as a species that favours eutrophic conditions or conditions with organic pollution (Armitage et al 1995; Edwards 1985; Gaufin & Tarzwell 1956). The organic load of the Dommel is high, and therefore supports the high densities of *C. riparius* recorded during summer at the reference site DEG (observed maximum 42,797 individuals m\(^2\)) and the first polluted location Neerpelt. On the other hand, dissolved metal concentrations were usually very high at Neerpelt during 1995, and regularly far exceeded chronic NOEC-values for growth, reproduction and mortality (Postma et al 1994; 1995b; Timmermans et al 1992). This is in contrast with the observed high densities at especially the first polluted location Neerpelt of almost 75,000 individuals m\(^2\) in November 1995. No significant differences in either seasonal dynamics or densities could be detected between the reference location and the first polluted station. For the further downstream located second polluted site, however, differences from the reference site were significant for all larval instars as well as for total larval densities. In general, factors like physical habitat characteristics or a different species composition can well contribute to the observed site specific differences. However, except for metal concentrations (table 2.1), no major differences in a diverse set of principal water and sediment characteristics along the research tract in River Dommel are recorded (Postma 1995). In addition, no major differences in species composition could be traced and are, therefore, not the most likely explanation for the observed difference between the different pattern of abundance of *C. riparius* larvae at the most downstream site. Consequently, the high cadmium and zinc concentrations in water and detritus seemed to affect the seasonal dynamics of *C. riparius* further downstream more than at the first polluted site. It could be hypothesised that the midges at the first polluted site were better adapted to metals than those further downstream. This is not a likely explanation because occasionally, for instance at the beginning of September
1995, almost no larvae were present at the first polluted site, contrary to the expectations based on high densities of first and second instar larvae just before, in August. At this specific time of the year, simultaneous measurements of cadmium in detritus suddenly increased by more than four times and measurements of zinc increased by more than a factor two, compared with the average values. At the same time, more than 60% of the *C. riparius* larvae present, consisted of first and second instar larvae and it is generally known that these younger instars are much more sensitive to cadmium than older instars (Williams et al 1986). A tentative explanation, therefore, could be that the local first and second instar chironomids present were eradicated by the sudden increase in metal concentrations in detritus and this could well explain the lack of expected third instar larvae. A comparable situation existed at the second polluted downstream site at the end of July, when more than 60% of the *C. riparius* larvae consisted of first instar larvae. During this period, concentrations of zinc and cadmium in detritus also sharply increased. Again, it seems most likely that the sudden decrease in density was caused by high metal concentrations in detritus at times when a large proportion of the *C. riparius* larvae present consisted of sensitive first instar larvae.

It is concluded that average levels of metal contamination in the Dommel did not significantly affect either the life history or the total larval densities of *C. riparius* present. Sudden peaks in metal contamination, however, with concurrent presence of a large proportion of sensitive first and second instar larvae, can most likely affect the population. It is therefore suggested, that only the observed high metal concentrations in detritus created a high selection pressure for metal adaptation in the field situation, most likely by causing massive mortality of young larvae.

**influence of larval drift**

To make a rough estimate of the impact of non-tolerant drifting larvae entering the first metal-exposed site, a daily larval input can be calculated using the following assumptions: 1) Larval drift is constant during a period of 24 hours; 2) The distance travelled by larval chironomids is 100 metres at
a maximum and thus migrating larvae settle out of the drift in the polluted section; 3) Downstream chironomid density is uniform and midge habitat is estimated as two square metres per metre river, concurrent with the zone close to the river banks where organic material settles. It should be noted that the method used to measure drifting larvae does not capture all spatio-temporal variability. The calculated larval influx should be seen as a conservative estimate. Assumption 1 for instance, may lead to underestimated drift rates, because larval drift of some chironomids, including a *Chironomus* species, is known to be higher at night than during the day (Ali & Mulla 1979; Stoneburner & Smock 1979). In addition, also assumption 2 may lead to a conservative calculation because the distance of 100 metres is about the maximum recorded in literature for chironomids as well as for other drifting invertebrates (McLay 1970; Elliott 1971; Larkin & McKone 1985; Brittain & Eikeland 1988). Furthermore, the extent of larval drift is also substantially underestimated by the use of a 250 μm driftnet, through which a good proportion of living first and second instar larvae would pass (Storey & Pinder 1985). When considering the influence of all spatio-temporal variability as discussed above, more larvae would be caught and thus, a greater influence should be calculated. The calculations of daily influx percentages were made by comparing the calculated daily number of drifting non-tolerant larvae to the actual number of larvae present at the receiving, metal-exposed site.

Estimated daily input of non-tolerant larvae at the first downstream site, sometimes exceeded even 100% of the standing stock present, especially between February and April when larval densities at metal-exposed sites are low and the number of drifting individuals peaked. Even when larval densities are high, for instance during July-September, the influence of upstream larvae in the downstream metal-exposed site amounts to 5-10% of the standing stock per day. Although roughly estimated, it is clear that the impact of drifting non-tolerant larvae entering the metal-exposed sites just downstream from the point source is substantial. Therefore, any effects arising from the effects of metal contamination on exposed larvae would
likely to be masked by the presence of large numbers of immigrants from upstream sites.

During the second half of 1995, the population of *C. riparius* at the second polluted location did not recover from its sudden density decrease. In contrast, after the sudden drop at the end of August, densities at the upstream polluted station increased within a month to more than 20,000 individuals m$^{-2}$. This difference in recovery can be explained by the drift of larvae from unpolluted sites upstream. During July-September 1995, the daily influx peaked, when an estimated number of 15,000 larvae were entering the polluted reach every hour. The influence of this larval drift on the second polluted location, situated circa seven kilometres downstream, was most likely less important. This may explain the observed differences in recovery rates as well as in densities and seasonal dynamics between the two metal-exposed sites, and the almost identical seasonal dynamics of the reference site and the first polluted location.

High immigration rates of upstream non-tolerant larvae might also indirectly affect the overall level of metal tolerance present in the downstream chironomids. Due to high drift rates, genetic uniformity of chironomids inhabiting upstream and downstream locations is to be expected and was measured on one occasion (Raijmann & van Grootveld 1997). In addition, the presence of adult midges can increase the genetic uniformity further. Although it is generally thought that drifting larvae normally represent the major part of the total gene flow compared to the minor dispersal of the short living and weak flying imagoes (Davies 1976), it is likely that there will be a certain amount of genetic mixing, especially caused by the females, which may move some distance to mate and oviposit (Williams & Williams 1993). Judging the high drift rates, the question arises if there can be a local metal-adapted subpopulation present at polluted sites. It seems likely that metal adaptation is re-established again and again after periods of increased metal stress and mortality of first and second instars. However, once these tolerant specimens occur, as showed by Postma (1995), they can also be lost from the metal polluted sites due to larval drift. There is no evidence suggesting that metal-adapted specimens are less prone to
drift than non-adapted specimens. Consequently, the metal-adapted individual midges are often present only in low densities and abound only on special occasions, such as found for downstream sites after a period of intense metal stress and low import of non-exposed specimens. Their specific life cycle trait such as indicated by Postma et al (1995a) may, therefore, be apparent in the seasonal dynamics on rare occasions only.

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References


SEASONAL DYNAMICS AND LARVAL DRIFT


