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The influence of temperature on emergence periods of Chironomidae (Diptera) from a shallow Danish lake

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A window trap (800 cm^2 catching area) was operated at the shore of the eutrophic and shallow Lake Stigsholm during 1993-1994 and emptied every two weeks from April to October. An average of 18,000 adult chironomids belonging to 59 species were caught each year. Females dominated the catches with a 1 ♂:3 ♀ ratio in 1993, whereas the opposite ratio was found in 1994. Tanytarsini was the dominant group constituting 85% of the total catch. Tanypodinae (3%), Orthocladiinae (7%) and Chironomini (5%) were represented equally each year. Although adult chironomids were caught throughout the sampling periods, a distinct peak occurred in May-July, when 90% of the emergence took place. In August-September emergence dropped to 8%, while the remaining 2% emerged during April and October. Most species had flight periods of several months, but with distinct emergence peaks during a shorter period of 2-6 weeks. A majority of the species were univoltine, but a few were bivoltine. Orthocladiinae dominated the catches during the low-season emergence months of April and October, while the other subfamilies were restricted to May-September. A rapid increase in water temperature from 12 to 18 °C in late May 1993 caused a mass emergence of "summer species" such as *Psilotanypus rufovittatus*, *Cladotanytarsus* spp. and *Tanytarsus* spp. in late May and early June. In 1994, a similar increase in temperature from 14 to 22 °C in early July triggered a mass emergence of the same species. Most Chironomini had "fixed" emergence periods independent of the water temperature.

Key words: Chironomidae, emergence, voltinism, shallow lakes, benthic communities

Introduction

Detailed identification of chironomid species was needed for a paleolimnogical study on chironomid headcapsules in shallow lakes (Brodersen and Lindegaard 1997). Therefore, in order to identify the chironomid species a window trap was operated on the shore of Lake Stigsholm during 1993 and 1994. Because adult chironomids are short-lived their swarming period may more or less coincide with their emergence period and regular catches of adult chironomids in traps during a year can therefore reveal both the number of species and their voltinism.

This paper describes the emergence of chironomids from the shallow Lake Stigsholm in two successive years and correlates differences in emergence to differences in temperature between years.

Study area

Lake Stigsholm is situated in central Jutland (9°30' E, 55°58' N). It is a small (0.21 km^2) and shallow lake with a maximum water depth of 1.1 m and a mean water depth of 0.8 m (Fig. 1).

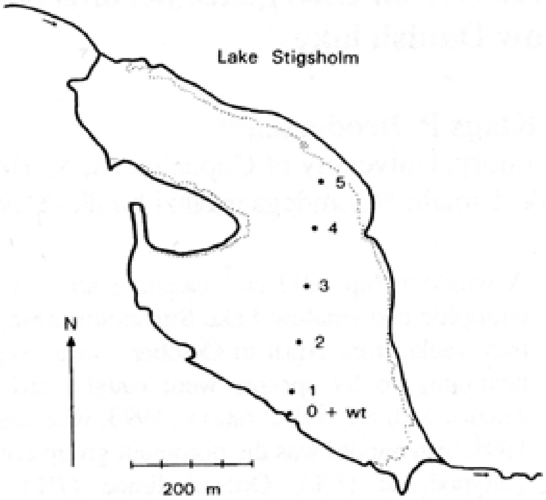


Fig. 1. Map of Lake Stigsholm (9°30' E, 55°58' N) showing the location of the window trap (wt). Dotted line indicates the extension of the reed belt. Numbers 0-5 indicate stations for benthic sampling.

The catchment area is 6.3 km^2 and the lake is surrounded by common pastures grassed by cattle and horses. Reed belts are present at most of the lake border except at the southern border where grazing prevents growth of *Phragmites*. The water retention time is only five days. The lake is eutrophic with a mean annual total phosphorous content of 150 µg P l^{-1} and a mean chlorophyll *a* content of 54 µg l^{-1}. The Secchi depth only exceeds 1.1 m half the summer (Søndergaard et al. 1996). Submerged macrophytes (*Potamogeton pectinatus* L., *Callitriche hermaphroditica* L. and *Elodea canadensis* Rich.) and filamentous algae are present all over the bottom, but the abundance was low during 1993 and 1994 allowing for a high production of benthic algae.

Methods

A window trap constructed and handled as described by Jónsson et al. (1986) was placed next to the shore in the southern end of the lake (Fig. 1). The catching area was 800 cm^2 and the holding compartments were filled with 4% formaldehyde. During spring ethylene glycol was added to prevent ice formation. The trap was emptied every two weeks from April to October and chironomids were stored in 70% ethanol.

To monitor the benthic fauna, sediment core samples were taken monthly during 1995 and 1996 at six stations across the lake (Fig. 1). These samples were process through a 200 µm screen and animals stored in 4% formaldehyd. The chironomid larvae from the 1995 samples were used to evaluate the effectiveness of the window trap.

Water temperature was measured 13 times in 1993 and 15 times in 1994. Due to the small volume of water in Lake Stigsholm the water temperature was closely related to air temperature (Fig. 2). Continuous measures of air temperature (daily mean) were available from a local weather station 15 km from Lake Stigsholm. The measured water temperature was best correlated to the average air temperature of the day plus the two previous days ($r^2 = 0.91$). This correlation was used to calculate the continuous water temperature during 1993 and 1994 (Fig. 3).

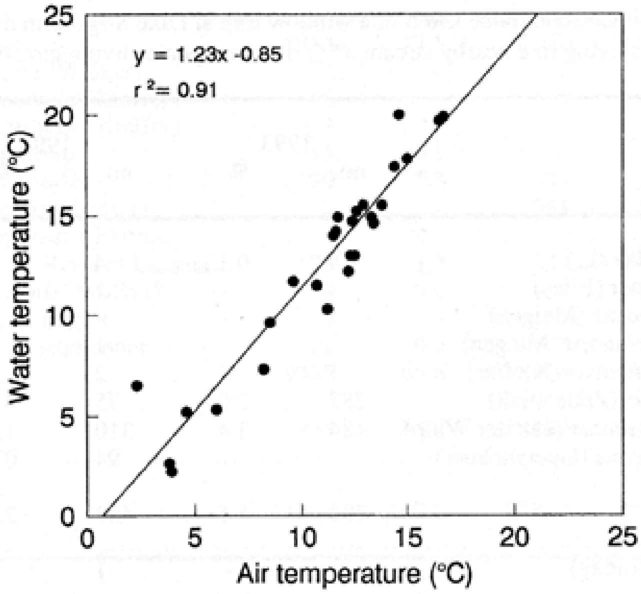


Fig. 2. Correlation between measured water temperature of Lake Stigsholm and daily mean air temperature recorded by a local weather station 15 km from the lake.

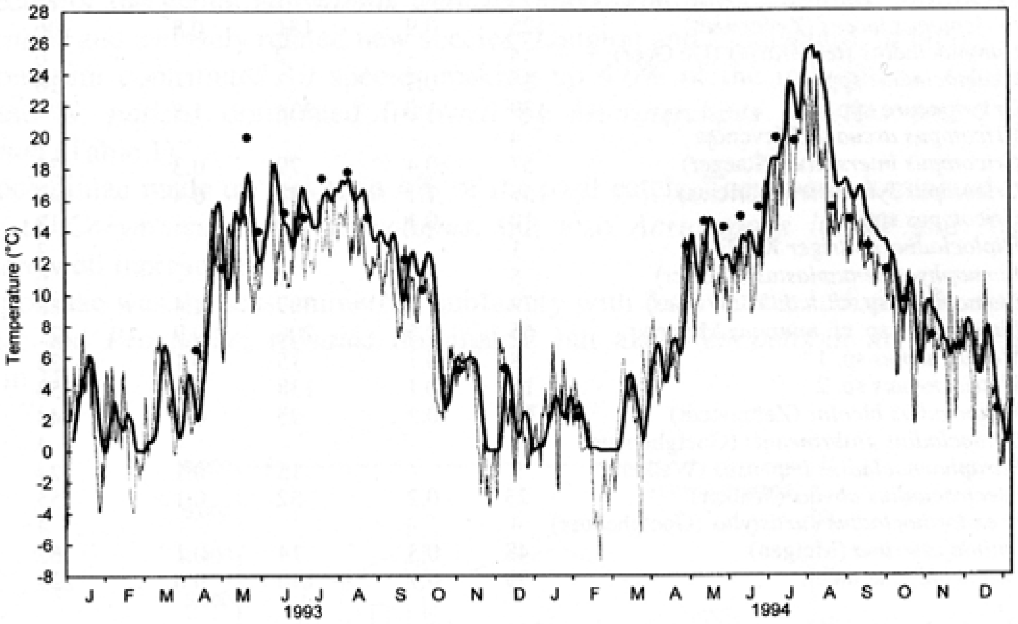


Fig. 3. The daily mean air temperature (grey line) and a seven days running mean of water temperature (black line) calculated from air temperature by the correlation shown in Fig. 2. Black dots are the actual measured water temperature.

Results

About 37,000 chironomids representing 59 taxa were collected by the window trap during 1993 and 1994 (Table 1). Six species are considered exclusively running water species in Denmark (marked with an (*) in Table 1). They originated from a nearby stream and occurred in very low numbers. Nine taxa were of terrestrial or semiterrestrial origin (marked with (**) in Table 1); they all occurred in low to moderate numbers. The remaining 45 species made up more than 97% of the total catch, and were considered true lake species.

Female chironomids made up 78% of the catch in 1993, but only 37% in 1994. The Tanypodinae *Procladius signatus* and *Psilotanypus rufovittatus* were dominated by females both years, while *Acricotopus lucens* was dominated by males both years.

The tribe Tanytarsini contributed about 85% of the individuals of which half were females. The female Tanytarsini were not separated into genera. The genus *Cladotanytarsus* was especially numerous with 72%. At least three species (*C. atridorsum* Kieffer, *C. mancus* (Walker) and *C.*

Table 1. Total number of adult Chironomidae taken in a window trap at Lake Stigsholm during April - October 1993 and 1994. (*) denotes species living in a nearby stream. (**) denotes species living terrestrial or semiterrestrial.

		1993		1994		Total	
	Species	no.	%	no.	%	no.	%
	Ablabesmyia monilis (L.)	9	0.1	4	-	13	-
	Anatopynia plumipes (Fries)	-	-	1	-	1	-
	Clinotanypus nervosus (Meigen)	1	-	-	-	1	-
*	*Conchapelopia melanops* (Meigen)	-	-	1	-	1	-
	Monopelopia tenuicalcar (Kieffer)	1	-	2	-	3	-
	Procladius signatus (Zetterstedt)	287	2.0	75	0.3	362	1.0
	Psilotanypus rufovittatus (van der Wulp)	484	3.4	310	1.4	794	2.1
	Xenopelopia nigricans (Goetghebuer)	-	-	94	0.4	94	0.3
Tanypodinae, total		782	5.5	487	2.1	1269	3.4
*	*Diamesa tonsa* (Haliday)	-	-	1	-	1	-
Diamesinae, total		-	-	1	-	1	-
	Acricotopus lucens (Zetterstedt)	125	0.9	181	0.8	306	0.8
**	*Camptocladius stercorarius* (De Geer)	4	-	2	-	6	-
	Chaetocladius spp.	15	0.1	3	-	18	-
	Corynoneura spp.	139	1.0	338	1.5	477	1.3
	Cricotopus arcuatus Hirvenoja	4	-	-	-	4	-
	Cricotopus intersectus (Staeger)	57	0.4	79	0.3	136	0.4
	Cricotopus sylvestris (Fabricius)	157	1.1	83	0.4	240	0.6
	Cricotopus spp.	12	0.1	6	-	18	-
*	*Diplocladius cultriger* Kieffer	1	-	2	-	3	-
**	*Limnophyes pentaplastus* (Kieffer)	5	-	1	-	6	-
**	*Limnophyes* sp. cf. *habilis* (Walker)	179	1.3	309	1.4	488	1.3
**	*Limnophyes* sp. cf. *minimus* Meigen	65	0.5	206	0.9	271	0.7
**	*Metriocnemus* sp. 1	8	0.1	15	0.1	23	0.1
**	*Metriocnemus* sp. 2	15	0.1	138	0.6	153	0.4
	Nanocladius bicolor (Zetterstedt)	49	0.3	95	0.4	144	0.4
	Orthocladius glabripennis (Goetghebuer)	4	-	-	-	4	-
**	*Paraphaenocladius impensus* (Walker)	9	-	15	0.1	24	0.1
	Psectrocladius obvius (Walker)	23	0.2	32	0.1	55	0.1
**	*Pseudorthocladius curtistylus* (Goetghebuer)	4	-	-	-	4	-
**	*Smittia atterima* (Meigen)	48	0.3	14	0.1	62	0.2
	Orthocladiinae indet.	99	0.7	130	0.6	229	0.6
Orthocladiinae, total		1022	7.2	1649	7.2	2671	7.2
	Camptochironomus tentans Fabricius	39	0.3	105	0.5	144	0.4
	Chironomus plumosus L.	4	-	7	-	11	-
	Chironomus spp.	7	-	30	0.1	37	0.1
	Cryptochironomus redekei (Kruseman)	1	-	1	-	2	-
	Demicryptochironomus vulneratus (Zetterstedt)	4	-	-	-	4	-
	Dicrotendipes lobiger (Kieffer)	5	-	-	-	5	-
	Dicrotendipes modestus (Say)	5	0.4	8	-	63	0.2
	Dicrotendipes nervosus (Staeger)	10	0.1	-	-	10	-
	Endochironomus albipennis (Meigen)	24	0.2	44	0.2	68	0.2
	Glyptotendipes pallens (Meigen)	9	0.1	272	1.2	281	0.8
	Glyptotendipes paripes (Edwards)	24	0.2	484	2.1	508	1.4
	Microtendipes pedellus (De Geer)	43	0.3	134	0.6	177	0.5
	Parachironomus arcuatus (Goetghebuer)	-	-	15	0.1	15	-
	Parachironomus vitiosus (Goetghebuer)	1	-	-	-	1	-
	Pentapedilum sordens (van der Wulp)	-	-	20	0.1	20	0.1
	Polypedilum bicrenatum Kieffer	26	0.2	4	-	30	0.1
	Polypedilum laetum (Meigen)	16	0.1	22	0.1	38	0.1
	Polypedilum nubeculosum (Meigen)	158	1.1	40	0.2	198	0.5
	Stictochironomus sticticus (Fabricius)	12	0.1	54	0.2	66	0.2

Chironomini, total	438	3.1	1240	5.4	1678	4.5
Cladotanytarsus spp	1913	13.5	12167	53.3	14080	38.0
* *Micropsectra apposita* (Walker)	1	-	1	-	2	-
* *Micropsectra atrofasciata* (Kieffer)	6	-	1	-	7	-
* *Paratanytarsus austriacus* (Kieffer)	3	-	-	-	3	-
Tanytarsus lestagei group	15	0.1	-	-	15	-
Tanytarsus mendax Kieffer	190	1.3	183	0.8	373	1.0
Tanytarsus miriforceps (Kieffer)	-	-	233	1.0	345	0.6
Tanytarsus mancospinosus Ekrem, Reiss et Langton	473	3.3	521	2.3	233	2.7
Tanytarsus pallidicornis (Walker)	8	0.1	1	-	9	-
Tanytarsus usmaensis Pagast	1	-	1	-	2	-
Tanytarsus verralli Goetghebuer	28	0.2	7	-	35	0.1
Tanytarsini, females	9323	65.6	6315	27.7	15638	42.3
Tanytarsini, total	11961	84.2	19430	85.2	31391	84.8
Total Chironomidae	14203	100.0	22807	99.9	37010	99.9

lepidocalcar Krüger) were present, but it was not possible to separate the species with certainty. Seven species of the genus *Tanytarsus* were recorded. The most abundant *Tanytarsus* species was *T. mendax* and a closely related new species (Langton and Lindegaard, in prep.).

The Chironomini contributed 19 species making up 4.6% of the individuals. *Glyptotendipes paripes* and *G. pallens* dominated followed by *Microtendipes pedellus* and *Polypedilum nubeculosum* (Table 1).

The Orthocladiinae made up less than 4% of the total catch. They were dominated by species belonging to *Corynoneura* and *Cricotopus*, but also *Acricotopus lucens* and *Nanocladius bicolor* were well represented.

The Tanypodinae was the least numerous subfamily with 3.4% of the individuals. *Psilotanypus rufovittatus* and *Procladius signatus* dominated, but also *Xenopelopia nigricans* was fairly abundant in 1994.

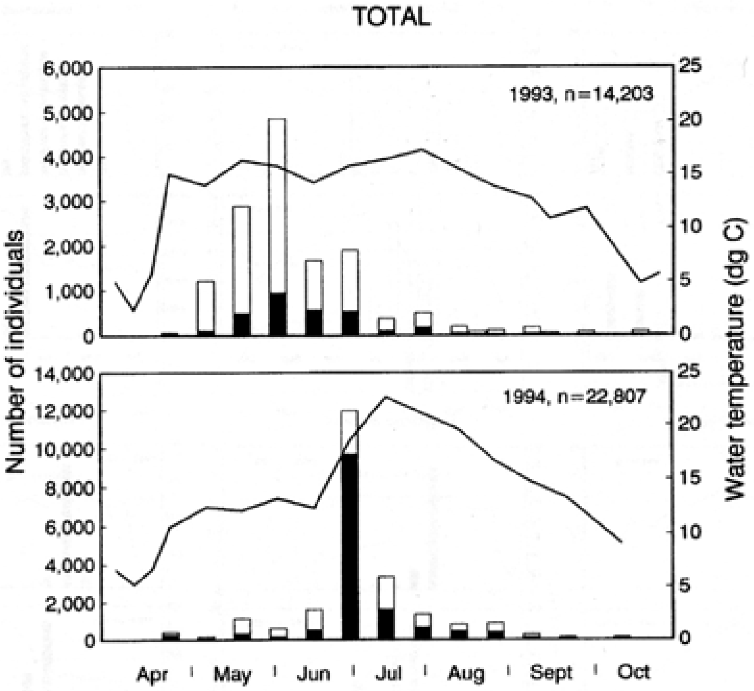


Fig. 4. The total catches of Chironomidae in 1993 and 1994 by window trap from Lake Stigsholm. Black and white columns indicate males and females, respectively. The average weekly water temperature is shown (solid line).

Adult chironomids were taken in the window trap from April till October, but a distinct peak occurred in May-July when 90% of the emergence took place (Fig. 4). The Tanytarsini characterized the peak, but all subfamilies were represented during these months. The emergence dropped to 8% during August and September, while the remaining 2% of the chironomids were caught in April and October. Chironomini dominated the emergence in August and early September, while Orthocladiinae dominated during April and October, except in 1994 when *Tanytarsus miriforceps* contributed to a peak in April.

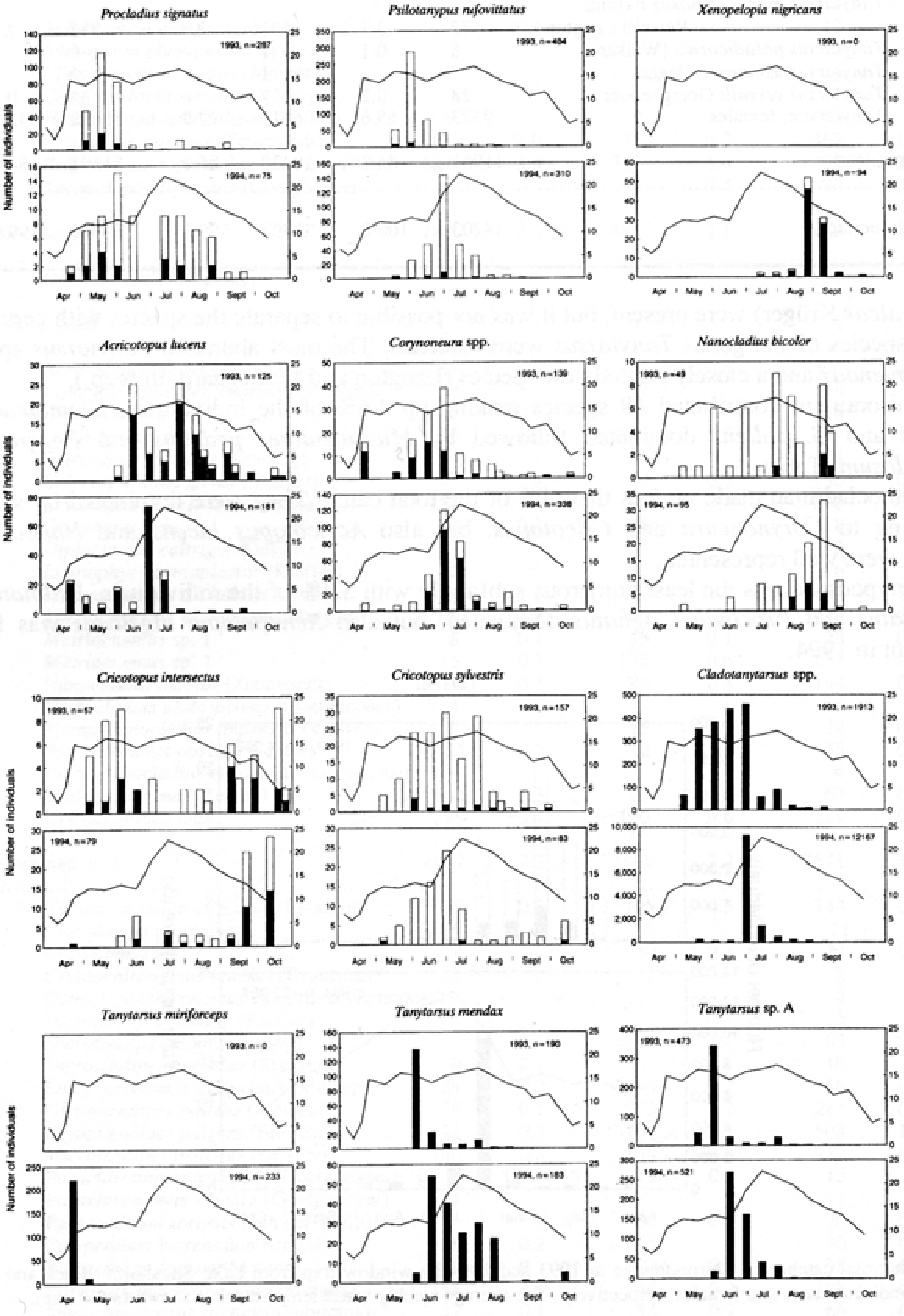
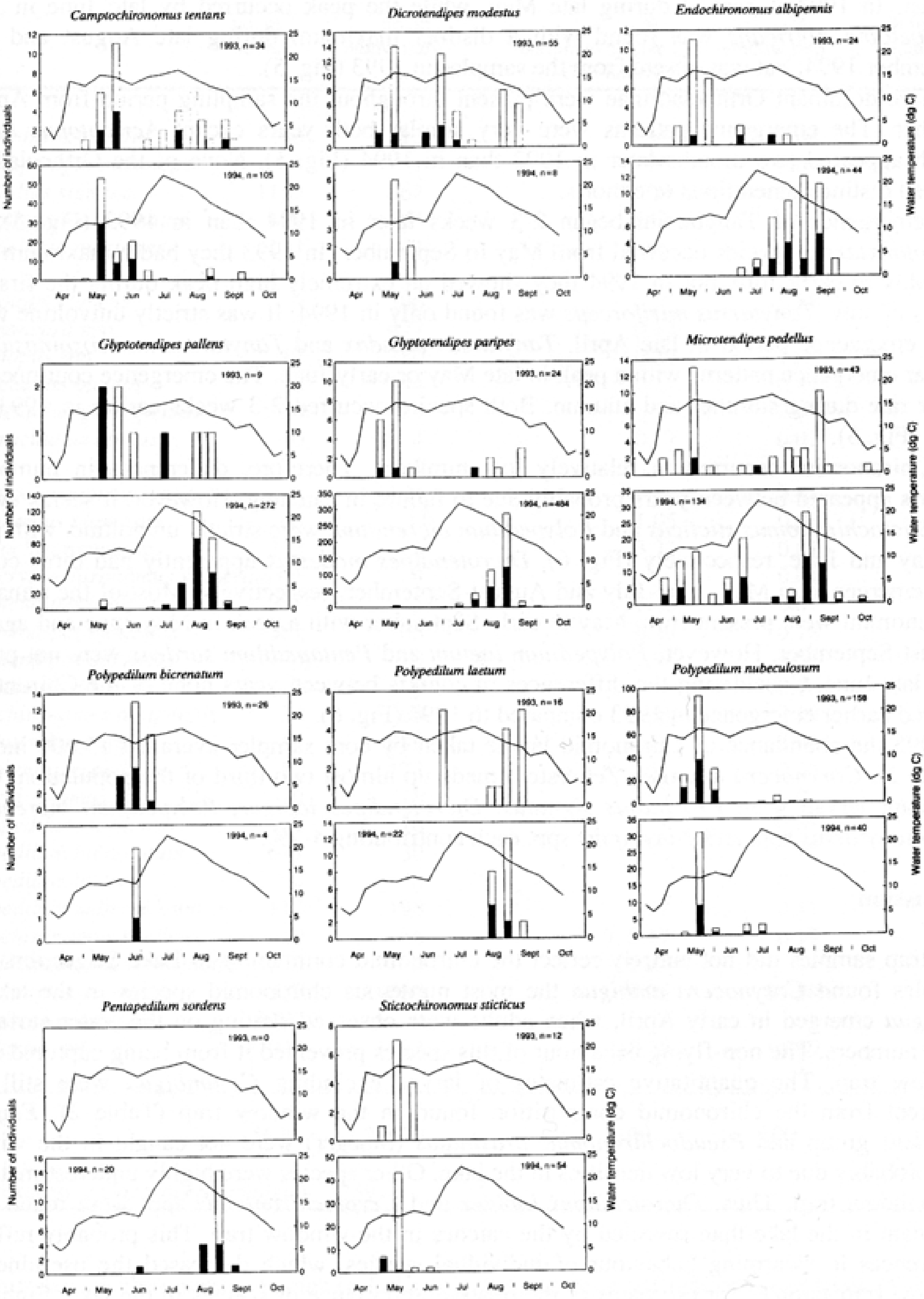


Fig. 5. The catches of the dominant Tanypodinae, Orthocladiinae and Tanytarsini in 1993 and 1994 from Lake

Stigsholm. Black and white columns indicate males and females, respectively. The average weekly water temperature is shown (solid line).

The emergence pattern differed between years. In 1993 the high peak of emergence took place from mid May to mid June, whereas in 1994 it appeared from mid June to mid July (Fig. 4). In both years the peak coincided with a strong increase in water temperature. In 1993 the temperature increased from about 6 to 18-20 °C within two weeks in late April and early May resulting in high emergence two weeks later, while an increase from 6 to 12-14 °C in the same period in 1994 did not trigger a high emergence. In 1994 an increase from 12 to 20 °C in late June coincided with the start of intense emergence (Fig. 4).



Camptochironomus tentans

Dicrotendipes modestus

Endochironomus albipennis

Glyptotendipes pallens

Glyptotendipes paripes

Microtendipes pedellus

Polypedilum bicrenatum

Polypedilum laetum

Polypedilum nubeculosum

Pentapedilum sordens

Stictochironomus sticticus

Fig. 6. The catches of the dominant Chironomini in 1993 and 1994 from Lake Stigsholm. Black and white columns indicate males and females, respectively. The average weekly water temperature is shown (solid line).

The emergence pattern of the 23 most numerous species are outlined in Figs. 5 and 6. Most species exhibit a long emergence period covering several months making it difficult to define different cohorts. This especially applies to the Tanypodinae, Orthocladiinae and Tanytarsini (Fig. 5), while the Chironomini more clearly could be described as uni- or bivoltine (Fig. 6).

Procladius signatus was present from April to September both years (Fig. 5). In 1993 it showed a distinct maximum in May, while in 1994 the occurrence during May-August was uniform. *Psilotanypus rufovittatus* had a slightly shorter emergence period and was found from May to August. In 1993 it peaked during late May, while the peak occurred by late June in 1994. *Xenopelopia nigricans* was found with a distinct maximum during late August and early September 1994, but was absent from the samples in 1993 (Fig. 5).

The five dominant Orthocladiinae were present throughout the sampling period from April to October. The emergence patterns were very similar both years except *Acricotopus lucens*, which appeared two months later in 1993 than in 1994 (Fig. 5). None of the Orthocladiinae showed distinct generations or cohorts.

The emergence of Tanytarsini began 2-3 weeks later in 1994 than in 1993 (Fig. 5). The *Cladotanytarsus* species occurred from May to September. In 1993 they had a maximum from late May to early July, but in 1994 they showed an extremely high peak during the first two weeks of July. *Tanytarsus miriforceps* was found only in 1994. It was strictly univoltine with a short emergence period in late April. *Tanytarsus mendax* and *Tanytarsus mancospinosus* had similar emergence patterns with a peak in late May or early June. The emergence continued at a lower rate during summer and autumn. Both species occurred 2-3 weeks earlier in 1993 than 1994 (Fig. 5).

All Chironomini occurred in relatively low numbers. Therefore, differences in number of cohorts appeared between years probably due to failure in catching. However, it seems evident that *Stictochironomus sticticus* and *Polypedilum bicrenatum* were strictly univoltine, with peaks in May and June, respectively (Fig. 6). *Dicrotendipes modestus* apparently had three cohorts with emergence in May, June-July and August-September, respectively. Most of the remaining Chironomini were present from May to early September with a peak in May-June and again in August-September. However, *Polypedilum laetum* and *Pentapedilum sordens* were not present until late June. Considering the differences in cohorts between years none of the Chironomini showed earlier emergence in 1993 compared to 1994 (Fig. 6).

In 1995 the abundance of chironomid larvae taken by core sampler averaged 15,600 ind. m^{-2} (Table 2). *Corynocera ambigua* Zetterstedt made up almost two third of the population. Other abundant larvae were *Procladius signatus*, *Dicrotendipes lobiger*, *Polypedilum bicrenatum*, *Cladotanytarsus* spp. and *Tanytarsus* spp. each contributing 4-7%.

Discussion

The trap samples did not entirely reflect the chironomid community in Lake Stigsholm. Core samples found *Corynocera ambigua* the most numerous chironomid species in the lake. *C. ambigua* emerged in early April, when adults were observed skating on the water surface in great numbers. The non-flying behaviour of this species prevented it from being captured in the window trap. The quantitative estimates of larvae excluding *C. ambigua* were still very different from the chironomid composition found in the window trap (Table 2). *Einfeldia dissidens* group and *Pseudochironomus prasinatus* (Staeger) were not caught in the window trap probably due to very low densities in the lake. Other species were highly underestimated by the window trap. Thus, *Dicrotendipes lobiger* and *Cryptochironomus* spp. were much more abundant in the lake than revealed by the catches in the window trap. This probably reflected differences in swarming behaviour of individual species, which decreased the usefulness of window trap samples for estimates of the relative importance of species in the lake. Eight taxa were caught in the window trap, but were not found in the core samples. Most of these occurred in relatively low numbers in the window trap, but *Acricotopus lucens*, *Nanocladius bicolor* and *Camptochironomus tentans* were expected to be present in the core samples. It was not likely that these species originated from nearby habitats.

Table 2. Average number of chironomid larvae m^{-2} taken in core samples at station 0-5 during 1995 compared to the proper lake species taken in the window trap in 1993 and 1994. The ratio % bottom / % window trap indicates if taxa are over- or under-represented in the window trap compared to their abundance in the lake.

Taxa	no. m^{-2} bottom	no. in window trap	% bottom exclusive *Corynocera*	% window trap	% bottom / % window trap
Ablabesmyia monilis	140	13	2.44	0.04	66
Conchapelopia melanops	3	1	0.06	0.01	19
Procladius signatus	1153	362	20.09	1.04	19
Psilotanypus rufovittatus	140	794	2.44	2.27	1
Xenopelopia nigricans	3	94	0.06	0.27	0.2
Acricotopus lucens	0	306	-	0.88	-
Corynoneura spp.	7	477	0.12	1.36	0.1
Cricotopus spp.	17	380	0.29	1.09	0.3
Nanocladius bicolor	0	144	-	0.41	-
Orthocladius glabripennis	0	24	-	0.07	-
Psectrocladius obvius	10	4	0.17	0.01	16
Camptochironomus tentans	0	144	-	0.41	-
Chironomus plumosus	60	11	1.05	0.03	34
Cryptochironomus sp.	213	2	3.72	0.01	620
Demicryptochironomus vulneratus	0	4	-	0.01	-
Dicrotendipes lobiger	943	5	16.43	0.01	1174
Dicrotendipes modestus	367	63	6.39	0.18	35
Dicrotendipes nervosus	170	10	2.96	0.03	106
Einfeldia dissidens gr.	3	0	-	0.06	-
Endochironomus albipennis	33	68	0.58	0.19	3
Glyptotendipes spp.	17	789	0.29	2.26	0.1
Microtendipes pedellus	87	177	1.51	0.51	3
Parachironomus spp.	0	16	-	0.05	-
Pentapedilum sordens	0	20	-	0.05	-
Polypedilum bicrenatum	617	30	10.74	0.09	125
Polypedilum laetum	0	38	-	0.11	-
Polypedilum nubeculosum	113	198	1.97	0.51	2
Stictochironomus sticticus	10	66	0.17	0.19	1
Pseudochironomus prasinatus	13	0	0.23	-	-
Cladotanytarsus spp.	577	14080	10.05	81.98	0.1
Corynocera ambigua	9900	0	-	-	-
Tanytarsus spp.	1043	1012	18.18	5.89	3
Total	15639	34970	100	100	
Total exclusive *Corynocera ambigua*	5739				

The number of chironomid species in Lake Stigsholm resembled that of other lakes (Table 3).

In seven north-west European lakes and reservoirs (including Lake Stigsholm) a total of 222 taxa were recorded by use of floating emergence traps, window traps or by sampling floating pupal exuviae. The species richness varied from 51 to 76, but only two taxa (*Cladotanytarsus* spp. and *Tanytarsus lestagei* group) were recorded in all seven lakes. The number of taxa common to the chironomid fauna in Lake Stigsholm varied from 19 to 26 in the six lakes with the highest similarity to Kempton Park East Reservoir (Table 3). However, a Cluster diagram based on Bray-Curtis similarities calculated on non-transformed species frequencies clustered Lake Stigsholm to the shallow Hjarbæk Fjord, but also to the stratified Lake Esrom (Fig. 7). Similarities to Kempton Park East Reservoir, Lake Erken, Gr. Plöner See and Målsjøen were low. Apparently maximum depth is not decisive for high similarities in the quantitative chironomid community.

Table 3. Number of chironomid species and individuals collected in emergence studies in seven north-west European lakes.

Lake	Max. depth m	No. of species	No. of individuals	No. of species common to Lake Stigsholm	References
Stigsholm	1	60	37,010	60	This study
Hjarbæk Fjord	1 (6)	51	82,136	24	Viborg Amtskommune (1987)
Kempton Park	7	53	35,188	26	Mundie (1957)
Målsjøen	13	73	2,124	19	Aagaard (1978)
Erken	20	76	18,447	19	Sandberg (1969)
Esrom	21	51	11,978	20	Jónsson (1987)
Gr. Plöner See	60	63	22,338	21	Humphries (1938)

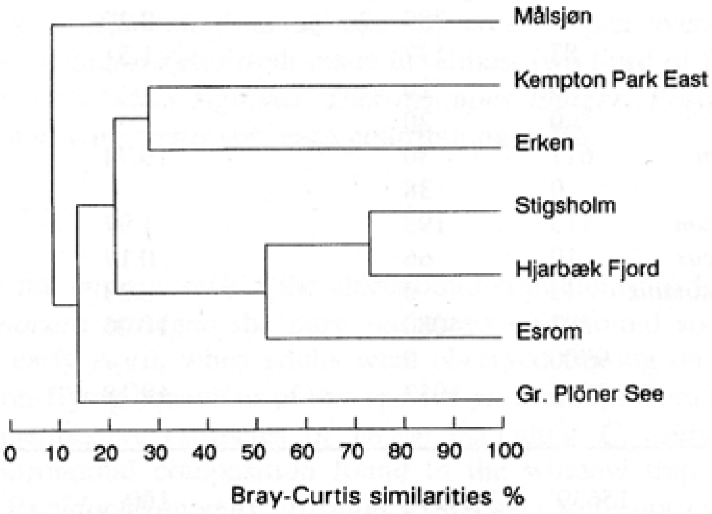


Fig. 7. A dendrogram based on Bray-Curtis similarities calculated on non-transformed frequencies of chironomids from seven north-west European lakes (references in Table 3).

Since the first study on emergence periods of chironomids in 1936 in Gr. Plöner See (Humphries 1938) many authors have contributed with studies on voltinism in chironomids.

Recently this knowledge has been summarized by Tokeshi (1995), who concluded that among a total of 125 chironomid taxa 33% are univoltine, 44% bivoltine and 18% multivoltine. The result from Lake Stigsholm does not differ significantly from this pattern.

From the total catches of chironomids it was evident that the peak in emergence took place in late May and June in 1993 and during June and early July in 1994 (Fig. 4). Most emergence studies, however, showed two peaks; the first peak coincided with that found in Lake Stigsholm and the second occurred in July-August (e.g. Sandberg 1969). A single emergence peak was also recorded by Titmus (1979), who in a shallow gravel pit in England found that a majority of chironomids emerged in late May and June. Apparently, the reason for this unimodale emergence curve was that the peaks of Tanytarsini in shallow lakes failed to develop a second, abundant generation. For example, Mundie (1957) found that *Tanytarsus mendax* (as *T. holochlorus* Edwards) had a distinct second generation in September at depths greater than 6 m in the Kempton Park East Reservoir. At lower depth only the June-July emergence took place. The reason for this pattern was not obvious, but an enhanced predation from juvenile fish in the shallow water during summer may be an explanation.

Humphries (1938) defined the terms spring, summer and autumn forms relating to the emergence period. These terms were further subdivided by adding early or late to the season. This terminology has been used by subsequent authors. In Lake Stigsholm only a few species obviously followed this system. Early spring forms were the univoltine species *Corynocera ambigua* and *Tanytarsus miriforceps* that emerged in early and late April, respectively. The univoltine *Stictochironomus sticticus* that emerged in May could be classified as a late spring form and *Polypedilum bicrenatum* could be an early summer form with emergence in June. *Xenopelopia nigricans* was an autumn form with a distinct peak in late August and early September. The remaining bivoltine Chironomini may be defined as summer and autumn forms. However, most Tanypodinae, Orthocladiinae and Tanytarsini all showed very long emergence periods and although some of them had one or more peaks they did not fit into this scheme. The reason for this is discussed below.

In his review of voltinism Tokeshi (1995) stated that the dominance of uni- and bivoltine species probably reflected that most life cycle studies have been performed in temperate areas; the implication was that temperature is one of the main controlling factors in determining the number of generations. Temperature determines the rate of development when other factors are optimal. Thus, Mackey (1977) found that most chironomids from the River Thames developed from eggs to adults within 1-3 weeks in the laboratory depending on the size of the species. This rate would allow for up to 20 generations in temperate areas. Similar or higher numbers of generations were estimated by Benke et al. (1984) in a subtropical stream. However, these high numbers have never been found in natural settings, and Lindegaard and Mortensen (1988) concluded that other factors (e.g. food, oxygen, current, inter- and intra-specific competition) influence the development time as much as temperature. The influence of this complex of factors is obviously not identical for all individuals of a given population. This results in very different development times, which expresses itself in a prolonged emergence period for many species. Only species with an endogenous factor determining growth or species living under very specific conditions (e.g. the profundal zone of stratified lakes) exhibit short synchronized emergence periods.

Despite the fact that temperature was only one of several factors determining emergence, it was apparent from the emergence patterns in Lake Stigsholm that an increase in temperature advanced the emergence especially of species without clearly defined generations. Such a general influence of temperature has also been noted by Titmus (1979) who correlated differences in emergence periods between two years to differences in spring temperature. A number of studies (e.g. Brundin 1949, Sandberg 1969) have shown that maximum emergence in lakes takes place by mid August when the water temperature are at maximum. This is valid for larger and deeper lakes, only, as maximum temperature in shallow lakes like Stigsholm can be reached early in the season. However, the raise in temperature from 6 to 12-14 °C in April 1994 in Lake Stigsholm did not trigger a mass emergence indicating that a certain minimum temperature is required for many species before hatching takes place. Humphries (1938) and Sandberg (1969) stated that the main emergence of Chironomini and Tanytarsini occurred at 15-16 °C and of Tanypodinae at 16-18 °C. This agreed with the findings in Lake Stigsholm, where the main emergence in both years started when the temperature exceeded 18 °C.

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