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Assessment of pollution history from recent sediments in Lake Vanajavesi, southern Finland. II. Changes in the Chironomidae, Chaoboridae and Ceratopogonidae (Diptera) fauna

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The subfossil remains of chironomids, chaoborids and ceratopogonids were analyzed from four short sediment profiles with the object of using them as palaeolimnological indicators of the development of Lake Vanajavesi during the industrial period of its history in the 19th and 20th Centuries. The present midge fauna (117 species) was sampled and the results were used as a reference material. 19 species new to Lake Vanajavesi were found only in the sediment profiles. Many of them were typical of oligotrophic lakes. A succession from an oligotrophic *Microspectra - Monodiamesa* community, through a eutrophic *Chironomus anthracinus* community, to a *Chironomus plumosus* community, was detected. The final stage of succession was the disappearance of the stationary bottom fauna, when the formation of annually laminated sediment became possible.

The results showed that a redeposition of shallow-water fauna on the deepwater bottoms was the most important factor affecting the composition and abundance of the subfossil fauna in the profiles. In the case of annually laminated sediment, plenty of midge remains were found, all of them redeposited. In this case the midge analysis indicates conditions in the littoral zone. The increase in numbers of littoral chironomids such as *Limnophyes* spp. was connected with the artificial lowering of lake water levels in the 18th and 19th Centuries. Midge analysis was found to be a useful palaeolimnological technique for indicating not only the typological development of the lake but also the past water level changes in the lake basin.

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Contents

1. Introduction

The advantages of the zoobenthos for monitoring changing aquatic ecosystems are well known. Biological organisms are able to integrate the effects of several environmental variables acting in concert, while chemical analyses usually represent measurements of single variables. Since benthic animals are mostly sedentary and have a long lifetime of up to several years in the case of the macrofauna and up to several months in the case of the meiofauna, a single sampling, or at most a few samplings, may be sufficient for long-term monitoring. Pelagic systems always require more frequent sampling.

The value of a long time series in the monitoring of lake zoobenthos has been demonstrated by Carr & Hiltunen (1965), Wiederholm (1974, 1978) and Kansanen & Aho (1981). In most cases, however, regular monitoring has not commenced until the process of eutrophication or pollution has proceeded for a long time, so that no reliable information on the natural state or early stages of change of a given recipient exists.

In the case of Lake Vanajavesi, which lies in southern Finland, the earliest zoobenthic investigations were made by Järnefelt (1929) in 1926, when the lake belonged to an oligotrophic (?) *Pontoporeia* or *Monodiamesa* benthic lake type. Regular monitoring began in the early 1960s, when the lake was of an already eutrophicated *Chironomus* type due to the heavy waste water loading (Kansanen & Aho 1981). There are extensive gaps in our knowledge of the benthic succession between 1926 and 1965. Differences in the sampling techniques used in older investigations and for more recent monitoring may also make direct comparisons difficult. A palaeolimnological study therefore constitutes the only means of accurately establishing the benthic succession.

One of the commonest groups of the benthic animals which leave identifiable remains as subfossils in lake sediments is the midges (defined as Chironomidae, Ceratopogonidae and the genus *Chaoborus* in the Chaoboridae, cf. Frey 1964, Stahl 1969). Research on midge remains in lake sediments has been reviewed by Stahl (1959, 1969), Frey (1964) and Hofmann (1971a). The benthic lake typology of Brundin (1949, 1956) and its modifications (Saether 1975, 1979, Wiederholm 1980) form a valid basis for stratigraphic interpretations of the development of deep, stratified basins, as shown by Hofmann (1971a, 1978), Warwick (1975, 1980) and Wiederholm & Eriksson (1979).

Chironomid analysis has also been applied to shallow, unstratified basins (Bryce 1962, Alhonen & Haavisto 1969, Carter 1977, Brodin 1982 and Dévai & Moldován 1983). As pointed out by Hofmann (1971b), the benthic lake typology of Brundin (1956) is not, as such, applicable to unstratified basins. Conclusions on the limnological development of shallow lakes must be drawn with special care and should take into account several other factors (e.g. climatic factors and lake siltation) which are independent of the eutrophication process.

In the first part of this study (Kansanen & Jaakkola 1985) four representative coring sites were selected on the basis of the mapping of surficial sediments. Several dating methods were tested in the four short sediment profiles. The results of the chemical analyses were given. The aim of the second part of the study is (1) to test the midge analysis as a palaeolimnological method, and, by combining the chemostratigraphic and biostratigraphic evidence, (2) to attempt to elucidate the historical changes in the general state of Lake Vanajavesi over the last 100-150 years.

2. Material and methods

2.1. Field work

Four short profiles (length 35-50.5 cm) were taken from Lake Vanajavesi for biostratigraphic analysis (Fig. 1). Profile KS1 was taken from the most polluted sub-basin, that of Kärjenniemenselkä, which receives the waste water load of the town of Valkeakoski and its industry. Profile RS2 was taken from Rauttunselkä, which is less polluted than Kärjenniemenselkä. Two profiles, VS1 and VS3, were taken from the main basin of the study area, called Vanajanselkä, which is eutrophicated but is still in a better condition than the other parts of Lake Vanajavesi.

A description of the study area and the coring operations were given by Kansanen & Jaakkola (1985). A Kajak-type gravity corer was used in sampling. At site KS1 the midge analysis between 0-26.5 cm was made from samples taken from a column of the sediment block frozen *in situ* using a sampler of the type described by Huttunen & Meriläinen (1978). The cores were sectioned into 0.5-2.3 cm thick slices.

In order to obtain reference material for the subfossil fauna, larvae of some quantitatively important profundal species were collected and reared to adults. The present fauna was also studied by collecting adults and pupal exuviae with a net from the shoreline, and with the aid of submerged funnel traps of the type designed by Brundin (1949). The funnel traps were placed at nine locations in Rauttunselkä and Vanajanselkä at water depths of 1, 3, 3, 6, 7, 8, 11, 14 and 20 m during the sampling periods

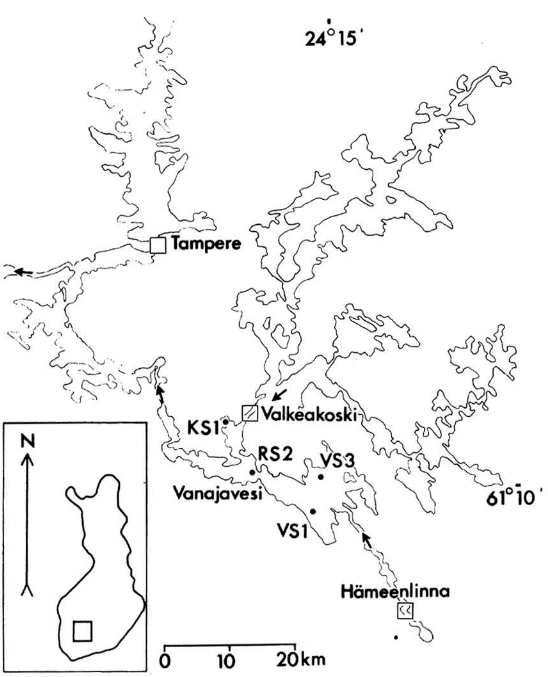

Fig. 1. Location of the study area in the southern drainage basin of the River Kokemäenjoki. Coring sites are indicated by black dots: KS1 Kärjenniemenselkä, RS2 Rauttunselkä, VS1 Vanajanselkä SW sub-basin and VS3 Vanajanselkä NE sub-basin. The direction of the water flow is indicated by arrows.

29.VI.-2.IX.1977 and 19.V.-1.X.1978.

Earlier collections of larval midges were made in 1965, 1966, 1967, 1971, 1974 and 1977 at standard depths of 1, 3, 5, 7, 10, 15 and 20 m using an Ekman-Birge grab and a 0.6 mm sieve. The methods and most of the results have been published by Kansanen (1981), Kansanen & Aho (1981) and Kansanen et al. (1984). Meiozoobenthos was studied by Kansanen (1981) using a Kajak corer and 0.1 mm sieve. The results of these studies were used as reference material for the present work.

2.2. Analysis of midge remains in sediments

A midge analysis was done on every sediment section of profile KS1 (thickness 0.5-1.2 cm, $n = 35$) and profile VS1 (thickness 1.2-2.3 cm, $n = 39$). In the case of profile VS3 every second section (thickness 1.0-2.0 cm, $n = 19$) was analysed, and from profile RS2 subsamples were taken from sections at about 5 cm intervals (thickness 1.3 cm, $n = 10$).

Subsamples of known volume (10 cm^3) were taken from the fresh sediment with a cut sampling syringe. In the case of frozen sediment (KS1), sections cut for biostratigraphic analyses were dried and weighed. The weight of the subsamples taken for analysis varied between 0.6-4.8 g. In the analysis of subsamples methods presented by Hofmann (1971a) and Warwick (1980) were applied.

Subsamples were deflocculated in 10% KOH at a low temperature (30°C) for two-three days. The sediment matrix was then removed by sieving through a fine-mesh sieve (100 µm). The material retained in the sieve, including midge remains, was washed in a basic solution of $Na_3PO_4 \cdot 12H_2O$ and then rinsed again through a fine-mesh sieve. The material retained in the sieve was laid evenly on a grooved disc apparatus designed by Hakala (1971) for the examination of sieved residues in meiozoobenthos sampling. The width of the grooves in the round disc was such that the entire width of the groove was visible using a 25× magnification under a Wild M-5 stereomicroscope. All midge remains (mainly head capsules and *Chaoborus* mandibles) were picked out carefully with fine forceps or needle probes. All remains were mounted directly on glass slides in polyvinyl lactophenol (10 specimens on the same slide). The use of this mounting medium saved a considerable amount of time, because in contrast to many other media polyvinyl lactophenol is water-soluble. The disc apparatus used in sorting was also superior to other methods in that it made rapid and systematic sorting of the sieved residue possible.

The total material consists of 4327 subfossil remains (3937 head capsules and 384 *Chaoborus* mandibles, 5 chironomid hypopygia and 1 pupal exuvia). The total volume of fresh sediment sieved was 1080 cm^3. The average number of midge remains in the usual sample volume of 10 cm^3 was 40.

3. Results

3.1. Present midge fauna of Lake Vanajavesi

At the present time 116 chironomid and 1 chaoborid species are known from Lake Vanajavesi (Table 1). The ceratopogonid fauna is at present poorly known. The number of species varies between sub-basins according to their trophic status and degree of pollution. In the most polluted Kärjenniemenselkä only 14 chironomid species have been found. The high number of species (80) in Vanajanselkä is due to the large size of the latter, the variety of habitats and generally better water quality compared to other parts of the study area. Oxygen depletion there is restricted to the hypolimnion.

When the bathymetric distribution of midge species is considered, one must take into account that all sub-basins of Lake Vanajavesi do not stratify regularly. There are often long stagnation periods during summer, when the lack of oxygen easily becomes a limiting factor due to the high production level and high waste water load. Even in the deepest depressions (max. 24 m) the water temperature may, however, often reach 14-15°C during late summer. This eliminates strictly cold-stenothermal species from the lake.

Table 1. Bathymetric and regional distribution of the midge species in Lake Vanajavesi in the years 1965-1978 (Kansanen 1981, Kansanen & Aho 1981, Kansanen et al. 1984 and own unpublished material). - A: Maximum observed larval abundance at each depth (ind/m^2) indicated. For observations of imagines, E = emerged adults found from funnel traps, * = larvae reared to adults. - B. Observation from different subareas: K = Kärjenniemenselkä, R = Rauttunselkä, V = Vanajanselkä and O = other basins. If only swarming males have been found on the shoreline, (S) is added after the symbol for the subarea.

	Bathymetric distribution				Regional distribution			
Taxon	Litt.	Sublittoral		Prof.				
	1 m	3-5 m	7-10 m	>12 m	K	R	V	O
C h i r o n o m i d a e								
Ablabesmyia longistyla Fittkau		6					V	
A. monilis-gr.	6		8	6			V	O
monilis (L.)		E	E	E		R	V	
phatta (Egger)						R(S)		
Anatopynia plumipes (Fries)	6		21					O
Macropelopia spp.		38					V	
Paramerina cingulata (Walker)							V(S)	
* Procladius sp. a (cf. ?choreus and ?cinereus)	165	647 E	351 E	357		R	V	O
Procladius sp. b (cf. signatus)	44	209 E	38	62		R	V	
Procladius sp. c (cf. nigriventris)	51	203 E	499 E	277	K	R	V	O
Procladius sp. d (cf. pectinatus		44		44 E			V	
* Procladius (Psilotanypus) lugens (Kieffer)	E		E	E		R	V	
Psectrotanypus varius (Fabricius)			6					O
Tanypus kraatzi (Kieffer)		38	13		K	R	V	O
Tanypus punctipennis Meigen		38 E	6		K	R		
Tanypus vilipennis (Kieffer)	10	62	101	24	K	R		O
Thiemenannimyia-gr.	82							O
Arctopelopia barbitarsis (Zett.)		E			•		V	
Conchapelopia melanops (Meigen)	E	E				R		
Potthastia gaedii (Meigen)	38						V	
Potthastia longimanus Kieffer	101	6					V	
* Monodiamesa bathyphila (Kieffer)		31	82	13			V	
Cricotopus spp.	44			13	K		V	O
albiforceps (Kieffer)		E	E			R	V	
annulator Goetghebuer		E	E			R	V	
bicinctus (Meigen)		E				R		
festivellus (Kieffer)		E				R		
intersectus (Staeger)		E				R		
reversus Hirvenoja		E				R		
sylvestris (Fabricius)		E	E			R		
triannulatus (Macquart)	E	E	E			R	V	
Epoicocladius flavens (Malloch)	13					R		
Heterotrissocladius grimshawi (Edwards)							V(S)	
Heterotrissocladius marcidus (Walker)	6	12					V	
Limnophyes spp.					K(S)			
Nanocladius bicolor (Zett.)		E	E	E		R	V	
Orthocladius spp.			6				V	
cf. excavatus Brundin							V(S)	
Paracladius conversus (Walker)	44					R	V	
Parakiefferiella bathophila (Kieffer)		E					V	
Parakiefferiella smolandica (Brundin)		E					V	
Psectrocladius psilopterus-gr.	65					R	V	
limbatellus (Holmgren)		E				R		
Camptochironomus tentans (Fabricius)					K(S)			
* Chironomus anthracinus Zett.	13	462	1237 E	3969 E		R	V	O
Chironomus cf. cingulatus Meigen						R(S)		
* Chironomus neocorax Wülker & Butler		254	881 E	754 E		R	V	
* Chironomus pilicornis (Fabricius)	+					R		
* Chironomus plumosus (L.)	932	1661 E	1579 E	456 E	K	R	V	O
Chironomus cf. pseudothummi Strenzke						R(S)		
* Cladopelma viridula (L.)	25 E	47 E	25 E	12 E	K	R	V	O
Cryptochironomus defectus-gr.	95	47	12	13	K	R	V	O
albofasciatus (Staeger)			E			R		
psittacinus (Meigen)		E	E			R		
supplicans (Meigen)		E					V	
Cryptochironomus ussouriensis Goetghebuer	49 E	24 E	25	K	R	V	O	
Cryptotendipes spp.	13						V	
usmaensis (Pagast)		E	E				V	
Demeijeria rufipes (L.)							V(S)	
Demicryptochironomus vulneratus (Zett.)	6	13	6				V	
Dicrotendipes spp.	216				K		V	
nervosus (Staeger)		E	E	E		R	V	
pulsus (Walker)		E		E			V	
tritomus (Kieffer)		E				R		
Einfeldia spp.	240	216	148	12	K	R	V	O
dissidens (Walker)			E			R	V	
Endochironomus albipennis (Meigen)		E	E			R	V	
Endochironomus impar (Walker)						R(S)		
Endochironomus intextus (Walker)						R(S)		
Glyptotendipes gripekoveni-gr.	938	6				R	V	O
gripekoveni Kieffer		E				R		
pallens (Meigen)		E	E			R		
paripes (Edwards)						R(S)		

Taxon	Bathymetric distribution				Regional distribution			
	Litt.	Sublittoral		Prof.				
	1 m	3-5 m	7-10 m	>12 m	K	R	V	0
Glyptotendipes mancunianus (Edwards)						R(S)		
Glyptotendipes signatus (Kieffer)		E				R		
Harnischia curtilamellata (Malloch)		25 E	6				V	
Microchironomus tener (Kieffer)	32	148 E	154 E	38 E	K	R	V	0
Microtendipes spp.	495	12					V	
chloris (Meigen)	E	E				R	V	
pedellus (de Geer)		E					V	
Nilothauma brayi (Goetghebuer)	6	31					V	
Parachironomus arcuatus (Goetghebuer)		E	E	E		R	V	
Parachironomus biannulatus (Staeger)						R(S)		
Parachironomus digitalis (Edwards)	E	E	E	E		R	V	
Parachironomus frequens (Johannsen)		E				R		
Parachironomus monochromus (van der Wulp)		E				R		
Parachironomus vitiosus (Goetghebuer)			E			R		
Paracladopelma camptolabis-gr.	6	6					V	
laminata (Kieffer)						R(S)		
Paralauterborniella nigrohalteralis (Malloch)	13	37	6				V	0
Phaenopsectra flavipes (Meigen)	6					R	V	
Polypedilum (Pentapedilum) sordens (van der Wulp)		E				R		
Polypedilum convictum-gr.			6			R	V	
cultellatum Goetghebuer						R(S)		
Polypedilum bicrenatum Kieffer	13	32	13 E			R	V	0
Polypedilum nubeculosum (Meigen)	171	37 E	13 E	E		R	V	0
Polypedilum pullum (Zett.)	25	E					V	
Pseudochironomus prasinatus (Staeger)	120						V	
Stenochironomus fascipennis (Zett.)						R(S)		
Stictochironomus psammophilus-gr.	368						V	
Stictochironomus sticticus (Fabricius)	533	101 E				R	V	
Cladotanytarsus atridorsum-gr.	76						V	0
atridorsum Kieffer		E					V	
difficilis Brundin	E	E				R	V	
wexionensis Brundin			E	E		R	V	
Cladotanytarsus mancus-gr.	609	82					V	
mancus (Walker)						R(S)		
nigrovittatus (Goetghebuer)			E				V	
Cladotanytarsus spp.	19		6			R		

Taxon	Bathymetric distribution				Regional distribution			
	Litt.	Sublittoral		Prof.				
	1 m	3-5 m	7-10 m	>12 m	K	R	V	0
Constempellina brevicosta (Edwards)	E	E	E			R	V	
Paratanytarsus spp.			6			R		
confusus Palmén						R(S)		
tenuis (Meigen)		E				R		
Stempellina almi Brundin		E					V	
Stempellina bausei (Kieffer)	63						V	
Stempellina subglabripennis (Brundin)	127 E	6 E	E	E		R	V	0
Stempellinella minor (Edwards)	70 E	19 E	10 E	E		R	V	
Tanytarsus aberrans Lindeberg	E		E			R		
Tanytarsus brundini Lindeberg		E	E	E			V	
Tanytarsus chipyensis Goetghebuer	92	6					V	
Tanytarsus curticornis Kieffer	25	E				R	V	
Tanytarsus eminulus-lestagei-gr.	418	92	19	19		R	V	0
eminulus (Walker)		E	E	E		R	V	
lestagei Goetghebuer	E	E		E		R	V	
longitarsis Kieffer	E		E			R	V	
palmeni Lindberg		E					V	
Tanytarsus lugens-gr.	13	19	44	6			V	
bathophilus Kieffer		E	E	E		R	V	
Tanytarsus mendax-gr.	82	542	49			R	V	0
occultus Brundin		E	E	E			V	
smolandicus Brundin			E			R	V	
Tanytarsus norwegicus Kieffer	E	E	E			R	V	
Tanytarus sylvaticus (van der Wulp)		E	E			R	V	
Tanytarsus usmaensis-gr.	25	6	19				V	0
usmaensis Pagast		E	E			R	V	
Tanytarsus verralli-gr.	216	19	19				V	0
debilis (Meigen)						R(S)		
Total number of species	53	80	57	32	14	73	80	27
Ceratopogonidae								
Bezzia-gr.	469	259	18	12	K	R	V	0
Chaoboridae								
Chaoborus flavicans (Meigen)	70	745 E	407 E	2233 E		R	V	0

The bathymetric distribution of the midge species (Table 1) shows that many species having their maximum abundance in the sublittoral zone (sensu Eggleton 1932) are found in low numbers in the profundal zone. Up to 32 species have been found from the profundal. Some of the species listed in Table 1 (*Parachironomus* spp.; Brundin 1949) do not live in the profundal, but have been collected from funnel traps, because even their fourth instar larvae are able to swim and often have a planktonic way of life.

The following midge species are quantitatively speaking most important in the profundal of Vanajavesi (Table 1):

Chironomus anthracinus
Chironomus neocorax
Chironomus plumosus
Procladius sp. a (near *choreus* and *cinereus*)
Procladius sp. c (near *nigriventris*)
Chaoborus flavicans

The maximum abundance of these species varied between 277-3969 ind/m^2 in the years 1965-1977.

According to Kansanen & Aho (1981), the eutrophic Vanajanselkä at present can be considered as the *Chironomus anthracinus* lake type of Brundin (1956). The dominance of this species varied in the profundal macrozoobenthos between 40-53 % in the period 1965-1977. The more polluted Rauttunselkä belongs to the *Chironomus plumosus* lake type (dominance of this species 11-20 %). Of the other species, *Microchironomus tener* in particular was typical of the *C. plumosus* community (Kansanen et al. 1984). The profundal of the most polluted Kärjenniemenselkä during these years was almost totally anoxic and devoid of macrozoobenthos. Only *C. plumosus* was detected in low numbers in 1977 from the lower depths of Kärjenniemenselkä. The high abundance and clear dominance of *C. plumosus* was typical of the sublittoral zone of Kärjenniemenselkä (dominance 90-100 %).

Kansanen et al. (1984) investigated the macrozoobenthos in 9 large lakes with several sub-basins in the southern part of the drainage basin of the River Kokemäenjoki, to which watercourse Lake Vanajavesi belongs. Most of these lakes were oligotrophic and had a *Tanytarsus lugens* type of community (Brundin 1956) in their profundal. The following chironomid species, which were common in the oligotrophic lake group, were lacking from the eutrophic lakes (Vanajavesi and Pyhäjärvi):

Protanypus morio
Heterotanytarsus apicalis
Pagastiella orophila
Stictochironomus rosenscholdi
Micropsectra spp.
Tanytarsus recurvatus- gr. (incl. *T. recurvatus* and *T. glabrescens*)

Of these species, *Protanypus morio, Stictochironomus rosenscholdi* and *Micropsectra* spp. are characteristic species in the *Tanytarsus lugens* community. *Heterotanytarsus apicalis, Pagastiella orophila* and *Tanytarsus recurvatus* are also known to prefer oligotrophic habitats (Brundin 1949). *Tanytarsus lugens* type larvae of the oligotrophic lakes most probably belonged to this species itself. *T. lugens* has not been found in Lake Vanajavesi. All larvae of the *T. lugens* type in Lake Vanajavesi were in fact *T. bathophilus* (Table 1).

On the other hand, there were several species in the eutrophic lakes which were absent from the oligotrophic group of lakes:

Anatopynia plumipes
Tanypus kraatzi
Tanypus vilipennis
Potthastia gaedii
Paracladius conversus
Cryptochironomus ussouriensis (syn. *C. nigridens* Chern.)
Einfeldia dissidens

Of these species, *Tanypus* spp., *Cryptochironomus ussouriensis*, and *Einfeldia dissidens* have been reported as occurring in eutrophic habitats (Chernovskii 1949, Saether 1979).

Quantitatively speaking, the density of larval midges is high in Lake Vanajavesi. In the profundal zone the highest densities of midges (0.6 mm sieve) were about 4700 ind/m^2. The density may also reach high values in the upper sublittoral zone. Kansanen (1981), using a 0.1 mm sieve, estimated that densities of larval Chironomidae were as high as 17 000 ind/m^2 at a depth of 3 m in Vanajanselkä.

3.2. Subfossil midge fauna of Lake Vanajavesi

3.2.1. Qualitative composition of the total material

A total of 3923 chironomid head capsules representing 86 taxa was identified from the sediment samples (Table 3). All chaoborid mandibles were those of *Chaoborus flavicans* (Meig.). The number of ceratopogonid head capsules was only 20 and these were not identified to species level. The most important chironomid genera quantitatively speaking were *Chironomus* (20.6% of the total material), *Procladius* (14.5%), *Tanytarsus* (8.5%), *Cricotopus* (6.2%) and *Psectrocladius* (3.5%). These genera together constituted up to 53% of the total number of chironomid specimens. Of the 86 taxa, 65 individually constituted less than 1% of the total material. Their proportion of the entire material was 30%.

The most important chironomid subgroups (subfamily or tribe) were Chironomini (37.9%) and Tanytarsini (20.4%). Prodiamesinae made up only 1% of the total remains. Of the total material, 6.3% was composed of unidentified Chironomidae. This group consisted of heavily fragmented head capsules of the second or third larval instars.

If the faunal lists of the present (Table 1) and subfossil (Table 3) midges are compared, a close similarity between them can be seen. There were, however, 19 species in the sediment samples which were new to Lake Vanajavesi (Table 2). Of these species, *Micropsectra* spp. was the most important taxon. Identification to the species level on the basis of larval characteristics was not possible. Two subfossil hypopygia found in the sediments were, however, identified as *M. insignilobus* or *M. lindebergi. Micropsectra* spp., *Phaenopsectra* (*Sergentia*) *coracina* and *Protanypus morio* occurred only in the lower layers of the cores. These species are typical to the *Tanytarsus lugens* community (Brundin 1956). Of the other species, at least *Heterotanytarsus apicalis, Zalutschia zalutschicola* and *Stempellinella brevis* have been reported as preferring oligotrophic waters (Brundin 1949, Saether 1979). On the other hand, many of the species listed in Table 2 obviously belong to the present fauna (e.g. *Corynoneura* spp., *Synorthocladius semivirens, Lauterborniella agrayloides*).

When the subfossil species are taken into account, the total number of chironomid species found in Lake Vanajavesi is 135.

Table 2. List of subfossil chironomid species new to Lake Vanajavesi found in the four sediment profiles. *N* = total number of remains, cm = sediment layer where the remains were located.

Taxon	*N*	cm
Micropsectra spp. (*insignilobus* or *lindebergi*)	83	16-48
Corynoneura spp.	59	0-47
Synorthocladius semivirens	25	4-48
Phaenopsectra (*Sergentia*) *coracina*	14	46-48
Heterotanytarsus apicalis	10	6-48
Pagastiella orophila	5	20-34
Protanypus morio	3	23-42
Lauterborniella agrayloides	3	4-46
Paratrichocladius rufiventris	2	0-38
Zalutschia zalutschicola	2	31-37
Paratendipes spp.	2	1-37
Xenochironomus xenolabis	2	9-44
Apsectrotanypus cf. *trifascipennis*	1	31-32
Psectrocladius calcaratus	1	2-3
Psectrocladius cf. *barbimanus*	1	41-44
Symposiocladius lignicola	1	41-42
Zalutschia cf. *mucronata*	1	31-32
Corynocera ambiqua	1	15-17
Stempellinella brevis	1	30-31

3.2.2. Comparison between present and subfossil faunas

The recent zoobenthos has been collected in earlier investigations from Lake Vanajavesi using the standard Ekman-Birge technique and a 0.6 mm sieve. Conclusions made regarding the benthic succession during the period 1926-1977 were based on this material (Kansanen & Aho 1981). Samples were generally taken in July-August. In order to evaluate the information value of subfossil fauna, the species composition obtained by the standard benthic sampling technique was compared with that obtained by the palaeolimnological method from the uppermost sediment layers. The composition of the subfossil chironomid fauna in the 0-6 cm sediment layer (average values) and the corresponding average composition of the live fauna (collected in 1971 and 1977) from the same places are presented in Table 4. According to Kansanen & Jaakkola (1985), the 0-6 cm layer was deposited in profile KS1 in 1971-1981. In other cores, which were affected by mixing, this layer was mainly deposited in the 1970s.

Table 3. Numbers (*N*) and relative abundance (%) of the subfossil chironomid head capsules, chaoborid and ceratopogonid remains in four sediment cores from Lake Vanajavesi. Names in parentheses refer to the corresponding taxonomic source. Species marked L are considered as shallow-water species.

Taxon	*N*	%	
1. *Chironomus anthracinus*-gr. (Hofmann 1971b)	562	14.3	
2. *Procladius* spp.	259	6.6	
3. *Cricotopus* spp. A (Hofmann 1971b)	245	6.2	L
4. *Chironomus plumosus*-gr. (Hofmann 1971b)	210	5.4	
5. *Procladius* sp. a	189	4.8	
6. *Tanytarsus* s. str. part (Hofmann 1971b)	153	3.9	
7. *Tanytarsus* spp.	118	3.0	
8. *Psectrocladius limbatellus*-gr. (Cranston et al. 1983)	110	2.8	L
9. *Microchironomus tener* (Kieffer)	101	2.6	
10. *Stempellinella minor* (Edwards)	85	2.2	
11. *Cladotanytarsus* spp.	83	2.1	L
12. *Micropsectra* spp.	81	2.1	
13. *Cladopelma viridula* (L.)	81	2.1	
14. *Polypedilum* s. str. spp.	78	2.0	
15. Pentaneurini spp. (Fittkau 1962)	74	1.9	
16. *Dicrotendipes* spp.	65	1.7	
17. *Corynoneura* spp.	59	1.5	L
18. *Glyptotendipes* spp.	58	1.5	L
19. *Parakiefferiella bathophila* (Kieffer)	53	1.4	
20. *Stempellina* spp.	45	1.1	
21. *Procladius* sp. c	41	1.0	
22. *Chironomus* spp.	38	0.97	
23. *Ablabesmyia* spp.	37	0.94	
24. *Procladius* sp. d	37	0.94	
25. *Procladius* (*Psilotanypus*) spp.	37	0.94	
26. *Parachironomus arcuatus*-gr. (Moller Pillot 1978)	36	0.92	L
27. *Tanytarsus chinyensis*-gr. (Hofmann 1971b)	36	0.92	L
28. *Monodiamesa bathyphila* (Kieffer)	35	0.89	
29. *Microtendipes pedellus*-gr. (Pinder & Reiss 1983)	33	0.84	L
30. *Harnischia curtilamellata* (Malloch)	32	0.82	
31. *Synorthocladius semivirens* (Kieffer)	25	0.64	L
32. *Cryptotendipes* spp.	20	0.51	L
33. *Psectrocladius psilopterus*-gr. (Cranston et al. 1983)	19	0.48	L
34. *Heterotrissocladius grimshawi* (Edwards)	18	0.46	
35. *Limnophyes* spp. (cf. *prolongatus* Kieffer)	16	0.41	L
36. *Paracladopelma camptolabis*-gr.	16	0.41	
37. *Endochironomus* cf. *albipennis* (Meigen)	15	0.38	L
38. *Phaenopsectra* (*Sergentia*) *coracina* (Zett.)	14	0.36	
39. *Constempellina brevicosta* (Edwards)	14	0.36	
40. *Tanytarsus pallidicornis*-gr. (Hofmann 1971b)	14	0.36	L
41. *Cryptochironomus defectus*-gr.	12	0.31	
42. *Phaenopsectra* s.str. spp.	12	0.31	L
43. *Stictochironomus sticticus* (Fabricius)	12	0.31	
44. *Nanocladius bicolor* (Zett.)	11	0.28	
45. *Demicryptochironomus vulneratus*	11	0.28	
46. *Polypedilum convictum*-gr. (Chernovskii 1949)	11	0.28	
47. *Heterotanytarsus apicalis* (Kieffer)	10	0.25	
48. *Paralauterborniella nigrohalteralis* (Malloch)	10	0.25	L
49. *Polypedilum nubeculosum* (Meigen)	10	0.25	
50. *Heterotrissocladius marcidus* (Walker)	9	0.23	
51. *Psectrocladius* spp.	9	0.23	L
52. *Polypedilum breviantennatum*-gr. (Chernovskii 1949)	9	0.23	
53. *Parakiefferiella smolandica* (Brundin)	8	0.20	
54. *Tanytarsus lugens*-gr. (Hofmann 1971b)	8	0.20	
55. *Polypedilum* (*Pentapedilum*) *sordens* (van der Wulp)	6	0.15	
56. *Polypedilum bicrenatum* Kieffer	6	0.15	
57. *Stempellina subglabripennis* (Brundin)	6	0.15	
58. *Procladius* sp. b	5	0.13	
59. *Paracladius conversus* (Walker)	5	0.13	L
60. *Pagastiella orophila* (Edwards)	5	0.13	L
61. *Endochironomus* cf. *intextus* Walker	4	0.10	L
62. *Protanypus morio* (Zett.)	3	<0.10	
63. *Orthocladius* spp.	3	"	
64. *Einfeldia* cf. *dissidens* (Shilova 1980)	3	"	
65. *Lauterborniella agrayloides* Kieffer	3	"	L
66. *Nilothauma brayi* (Goetghebuer)	3	"	L
67. *Paratanytarsus spp.*	3	"	L
68. *Tanypus vilipennis* (Kieffer)	2	"	
69. *Paratrichocladius rufiventris* (Meigen)	2	"	
70. *Zalutschia zalutschicola* Lipina	2	"	
71. *Paratendipes* spp.	2	"	L
72. *Xenochironomus xenolabis* Kieffer	2	"	L
73. *Micropsectra insignilobus* Kieffer or *lindebergi* Säwedal[1]	2	"	
74. *Stempellina bausei* (Kieffer)	2	"	
75. *Tanytarsus lestagei*-aggr. Lindeberg[1]	2	"	
76. *Apsectrotanypus* cf. *trifascipennis* (Zett.)	1	"	
77. *Psectrocladius calcaratus* (Edwards)[2]	1	"	L
78. *Psectrocladius* cf. *barbimanus* (Edwards)	1	"	L
79. *Symposiocladius lignicola* (Kieffer)	1	"	
80. *Zalutschia* cf. *mucronata* (Brundin)	1	"	
81. *Cryptochironomus ussouriensis* Goetghebuer	1	"	
82. *Parachironomus* sp. b	1	"	L
83. *Corynocera ambiqua* Zett.	1	"	L
84. *Stempellinella brevis* Edwards[1]	1	"	
85. *Stempellinella* sp.	1	"	
86. *Tanytarsus* sp. C (Hofmann 1971b)	1	"	
Tanypodinae	682	17.4	
Prodiamesinae	38	1.0	
Orthocladiinae	666	17.0	
Chironomini	1488	37.9	
Tanytarsini	800	20.4	
Unidentified Chironomidae	249	6.3	
Total Chironomidae	3923	100.0	
87. Ceratopogonidae	20		
88. *Chaoborus flavicans* (Meigen)[3]	384		
Total	4327		

[1] subfossil hypopygia [2] subfossil pupal exuvium [3] subfossil mandible

Table 4. Comparison between the percentage composition of the subfossil (S) fauna in the surficial sediment layers (0–6 cm) and the living (L) fauna at sites KS1, RS2, VS1 and VS3. The composition of the live fauna is based on samples taken by Ekman-Birge dredge and a 0.6 mm sieve in 1971 and 1977.

Taxon	KS1 S/L	RS2 S/L	VS1 S/L	VS3 S/L
Shallow-water species				
Pentaneurini	1.3/—	2.2/—	1.3/—	—
Corynoneura spp.	—	3.6/—	—	3.9/—
Cricotopus spp. A	10.3/—	10.8/—	1.3/—	3.9/—
Orthocladius spp.	—	0.7/—	—	—
Psectrocladius cf. *barbimanus*	0.6/—	—	—	—
Psectrocladius calcaratus	0.6/—	—	—	—
Psectrocladius limbatellus-gr.	13.5/—	—	1.3/—	1.3/—
Psectrocladius psilopterus-gr.	1.9/—	—	—	—
Synorthocladius semivirens	—	0.7/—	—	2.6/—
Cryptotendipes spp.	—	0.7/—	—	—
Endochironomus albipennis	2.6/—	0.7/—	—	—
Endochironomus intextus	0.6/—	—	—	—
Glyptotendipes spp.	0.6/—	4.3/—	—	1.3/—
Lauterborniella agrayloides	0.6/—	—	—	—
Microtendipes spp.	—	3.6/—	—	1.3/—
Parachironomus spp.	7.7/—	1.4/—	—	—
Paratendipes spp.	—	—	1.3/—	—
Phaenopsectra spp.	—	—	—	1.3/—
Cladotanytarsus spp.	—	5.8/—	—	2.6/—
Paratanytarsus spp.	1.3/—	—	—	—
Tanytarsus chinyensis-gr.	—	1.4/—	1.3/—	3.9/—
Tanytarsus pallidicornis-gr.	—	0.7/—	—	1.3/—
Total	41.6/0	36.6/0	6.5/0	23.4/0
Other species				
Ablabesmyia spp.	1.9/—	1.4/—	—	2.6/—
Procladius sp. a	—	1.4/2.5	3.8/0.8	2.6/0.4
Procladius sp. c	—	0.7/15.5	2.5/0.8	—
Procladius sp. d	—	—	3.8/1.0	—/2.2
Procladius spp.	1.9/—	2.9/—	2.5/—	5.2/—
Procladius (*Psilotanypus*) spp.	—	1.4/—	—	—
Tanypus vilipennis	—	—/5.1	—	—
Monodiamesa bathyphila	—	0.7/—	—	1.3/—
Nanocladius bicolor	0.6/—	—	1.3/—	—
Paracladius conversus	0.6/—	—	—	—
Parakiefferiella bathophila	1.3/—	2.2/—	—	—
Paratrichocladius rufiventris	—	—	—	1.3/—
Orthocladiinae spp.	0.6/—	1.4/—	—	—
Chironomus anthracinus-gr.	2.6/—	1.4/22.2	41.8/90.8	39.0/96.1
Chironomus plumosus-gr.	16.0/91.9	5.0/54.7	2.5/6.2	2.6/1.3
Chironomus spp.	—	0.7/—	1.3/—	—
Cladopelma viridula	9.0/—	5.0/—	—	—
Cryptochironomus defectus-gr.	—	0.7/—	—	—
Dicrotendipes spp.	1.9/—	2.9/—	—	5.2/—
Microchironomus tener	0.6/—	5.0/—	6.3/0.5	3.9/—
Paracladopelma camptolabis-gr.	—	—	1.3/—	—
Polypedilum (*Pentapedilum*) *sordens*	—	1.4/—	—	—
Polypedilum convictum-gr.	—	0.7/—	—	—
Polypedilum nubeculosum	2.6/—	—	—	—
Polypedilum spp.	0.6/—	0.7/—	—	—
Constempellina brevicosta	0.6/—	0.7/—	—	—
Stempellina spp.	—	2.2/—	3.8/—	1.3/—
Stempellinella minor	1.9/—	6.5/—	—	2.6/—
Tanytarsus spp.	7.6/8.1	15.8/—	11.4/—	6.5/—
Chironomidae spp.	7.7/—	2.2/—	11.4/—	2.6/—
Total %	100/100	100/100	100/100	100/100
Total *N*	156/27	139/472	79/2379	77/2871
Percentage similarity PS_c at each site between S and L	23.6 %	8.5 %	47.4 %	40.7 %
Coefficient of community *CC* between S and L	6.9 %	10.5 %	15.8 %	13.6 %
Distance of the coring site from shore (m)	240	120	900	1500
Water depth (m)	10	19	19	21

To evaluate the significance of a possible redeposition of littoral species remains, all species having a strong preference for the shallow-water zone were grouped together in Table 4. Species considered to belong to this group are listed in Table 3. The grouping was based on the literature (Brundin 1949, Reiss 1968, Hofmann 1971b) and personal observations (Table 1). It is clear that the littoral group defined in Table 3 is not complete. For example, the genus *Tanytarsus* may still include other strictly littoral species. Most of the other species can, however, be found, at least in low numbers, in the profundal zone.

At site KS1 in Kärjenniemenselkä the bottom samples taken in 1971 were totally devoid of bottom animals. A small number of *Chironomus plumosus* larvae and 1 *Tanytarsus* sp. were found from the profundal in 1977. Consequently, the high number of taxa occurring in the core samples is rather surprising. *Chironomus plumosus*-gr. is, however, the most abundant taxon (16% of the total material) here, as well as in the live fauna (91.9%). A high proportion of the shallow-water faunal components (41.6%) is typical of this profile. The composition of the subfossil and live faunas can be compared by using similarity indices. The percentage similarity of Renkonen (1938) is given by the formula:

$$PS_c = \Sigma \min (a', b'), \text{ where}$$

a' and b' are for each species the respective percentages of the total number of animals in samples A and B. The value of PS_c for KS1 was 19.8%. This index depends largely on the most common species. The coefficient of community (Jaccard 1902):

$$CC = 100c / (a + b + c), \text{ where}$$

a and b are the numbers of species in samples A and B, and c is the number of species occurring in both samples, depends to a greater extent than PS_c on rare species. The similarity between the subfossil and live faunas in KS1 was only 6.5%, when CC was used (Table 4).

At site RS2 in Rauttunselkä the live fauna in 1971 and 1977 was more diverse than in Kärjenniemenselkä (Table 4). The proportion of the most important genera in the live fauna, *Chironomus* (76.9% of the total live fauna) and *Procladius* (18.0%), was small in the subfossil fauna (7.1 and 5.0%, respectively). However, they belonged to the most abundant groups in the subfossil fauna, too. The subfossil fauna is very diverse compared with the live fauna, and the proportion of the shallow-water species is high (36.6%). The value of the PS_c-index between the live and subfossil faunas is lower than at other coring sites.

The proportion of the shallow-water species in the subfossil fauna is obviously lower at sites VS1 and VS3 in the large Vanajanselkä than at sites KS1 and RS2. The distance from the nearest shore at these sites is 900 m and 1500 m compared to 240 m and 120 m, respectively (Table 4). The dominant species of the live fauna at sites VS1 and VS3 in 1971 and 1977 was *Chironomus anthracinus*. This species, together with *C. neocorax* (*Chironomus anthracinus*-gr. s. Hofmann 1971b), constituted up to 90.8% and 96.1% of the live fauna. This taxon was clearly dominant in the subfossil fauna, too (41.8 and 39.0%). The proportion of the shallow-water species was only 6.5% of the total subfossil fauna at site VS1 and both the PS_c- and CC-indices showed a higher similarity between the live and subfossil faunas than elsewhere.

3.2.3. Profile KS1

The uppermost 35 cm of profile KS1 was examined (35 subsamples, 947 remains). The total number of chironomid head capsules (exx / 10 g dry matter) varied between 40–278 (Fig. 2). During the deposition period since the beginning of this century the density of remains has remained fairly constant. There is, however, a sharp increase in the uppermost layers, which are annually laminated and were deposited during the period 1970–1981.

As shown by Kansanen & Jaakkola (1985), the rate of sedimentation has varied remarkably at site KS1. In this case the deposition rate of midge remains per unit area is preferable because it provides a better picture of the real changes in the abundance of midges than the midge 'content', which is affected by dilution caused by a variable amount of annually deposited sedimentary matter (e.g. Digerfeldt 1972). In this case the estimates of sedimentation rates are accurate in the uppermost laminated layer (0–11.5 cm). Below this layer estimates are based on the C.R.S. model of ^{210}Pb distribution (Kansanen & Jaakkola 1985). The chironomid influx (expressed as individuals per m^2 per year) seems to have increased from the beginning of this century up to the end of the 1950s, when a sharp drop took place (Fig. 2). The influx fell

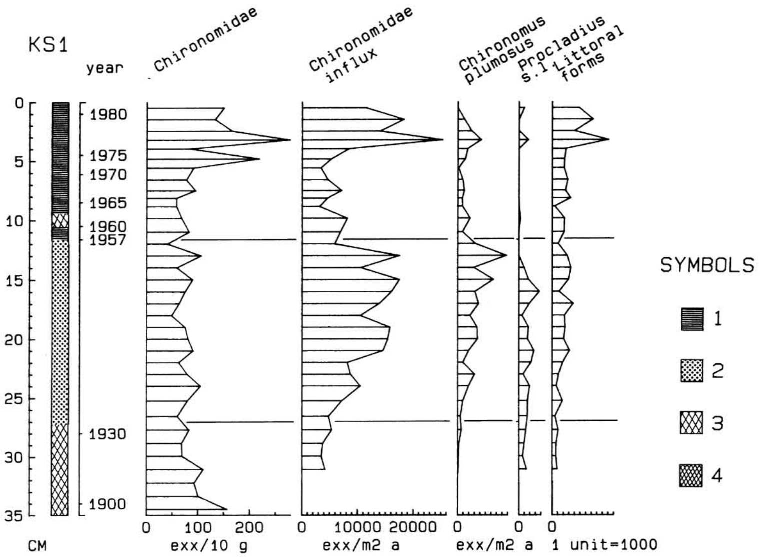

Fig. 2. The abundance (exx / 10 g d.m.) and influx (exx/m^2/year) of total chironomids and influx of *Chironomus plumosus*-gr., *Procladius* spp. and littoral species (cf. Table 3) in profile KS1. Time scale according to Kansanen & Jaakkola (1985). Symbols used for lithostratigraphy in the present study stand for: 1. black laminated sulphide clay-gyttja, 2. black or dark grey clay-gyttja with sulphide layers, 3. grey homogenous clay-gyttja, and 4. brown homogenous clay-gyttja.

from a level of 17 000 to a level of 3000-7000 in 1956-1957. There was, however, an increased chironomid influx after 1975 (up to 25 000).

If the influx values of two quantitatively important taxa (*Chironomus plumosus*-gr. and *Procladius* spp.) are considered, it can be seen that they closely follow the trend characterising the entire fauna. *Chironomus plumosus*-gr. rises evenly from the beginning of the century, when it was absent, up to a level of 8000-9000, but drops suddenly at the end of the 1950s to a level of 100-2300 (Fig. 2). There was a fresh increase after 1975, when influx values of 4000 were estimated. The influx of *Procladius* head capsules seems to have been slightly lower at the beginning of this century than it was after 1930 (time scale below 11.5 cm is rough). The highest influx values (3700) were estimated at the 16 cm level, from which *Procladius* remains suddenly disappear at the 13 cm level. This fall-off must have taken place during the 1950s before the reduction in *Chironomus* and the total fauna occurred (Fig. 2). A small amount of *Procladius* remains was again detected in the layers deposited after 1977.

The influx of head capsules of those chironomids which can be considered as strictly shallow-water species (for definition of this group, see Table 3) appears to have increased steadily from the beginning of the century, but over most of the core it has been rather constant (Fig. 2). It is interesting to note that there is no sharp drop after 1957, and that there is a sharp increase in the uppermost layers deposited in 1977-1981.

The successive changes in the composition of the subfossil faunal associations were examined by hierarchial classification analysis. In order to reduce the amount of 'samples' in the analysis each profile was divided into about 5 cm thick sequences (0-5, 5-10, 10-15 cm ...) and an average composition was calculated as a mean of the subsamples taken from the layer. The original data matrix was reduced in size by substitution of zero values for all entries lower than 2 % of the arithmetic mean density of subfossil remains in a single sediment layer. This was done to eliminate inconsistencies generated by the different sample sizes employed for different sediment layers (Clifford & Stephenson 1975). The percentage similarity of community (PS_c-index) was used as a similarity index. The classification was made as a group average clustering of sediment layers (Clifford & Stephenson 1975).

The results of the classification analysis of the sediment layers of profile KS1 are shown in Fig. 3. Four groups of sediment sequences were formed: group I, 0-10.5 cm; group II, 10.5-19.5 cm; group III, 19.5-30.5 cm; and group IV 30.5-35.0 cm. The result indicates clear vertical changes in the composition of the midge fauna.

The *F*-statistic (the ratio of the among-

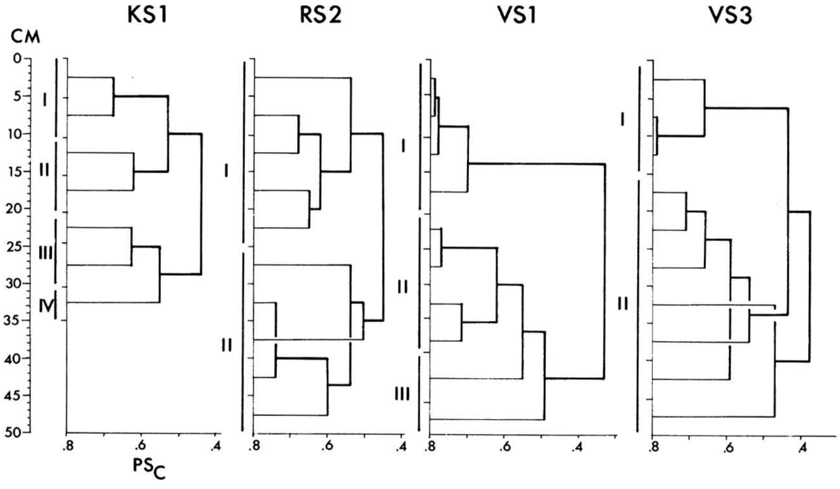

Fig. 3. Dendrograms showing the results of the hierarchial cluster analysis of the 5 cm thick sediment sequences on the abundances of subfossil midge remains. The vertical axis gives the sediment depth. On the horizontal axes is the value of the similarity index, which is the percentage similarity of Renkonen (1938). The group codes are indicated by Roman numerals in each profile.

groups to the within-groups variance of the relative abundance values after the arcsin-transformation) was used as an index of the degree to which the sediment sequence groups are defined by each subfossil taxon. *F*-values are not used here as tests of significance. All species which have an *F*-probability of less than 0.05 are listed in order of the magnitude of their contribution to the group definition in Table 5. The classification analysis thus reveals those species which are the best indicators of the succession in the sediment layers. The proportion of these indicator taxa in the total subfossil assemblage at various depths is shown in Fig. 4.

The diversity of the subfossil faunal association was calculated using the Shannon index:

$$H' = -\sum_{i=1}^{s} p_i \log_2 p_i,$$

where s = number of taxa, p_i = the proportion of the i^{th} taxon in the total fauna. The diversity of the subfossil fauna in profile KS1 is presented in Fig. 4, as well as the proportion of those species which can be defined as strictly shallow-water species (cf. Table 3).

Table 5. Comparison of sediment sequence groups defined in Fig. 3 on subfossil taxa in profile KS1. For further explanation see text. *** = $P<0.001$, ** = $P<0.01$, * = $P<0.05$.

Taxon	Mean % of the total fauna				
	Group I	Group II	Group III	Group IV	*F* (pr.)
cm:	0–10.5	10.5–19.5	19.5–30.5	30.5–35.0	(3.31 *df*)
1) *Procladius* sp. a	0.3	3.7	7.5	14.3	16.2***
2) *Parachironomus arcuatus*-gr.	10.0	1.0	1.7	0.9	12.9***
3) *Chironomus plumosus*-gr.	16.9	30.1	14.8	2.9	8.3***
4) *Procladius* (*Psilotanypus*) spp.	0.0	1.6	3.3	7.8	7.1***
5) *Cryptotendipes* spp.	0.0	0.0	0.7	4.0	6.6**
6) *Procladius* spp.	3.6	3.4	11.2	10.8	5.3**
7) *Microchironomus tener*	1.3	4.6	8.2	3.6	4.8**
8) *Psectrocladius* spp.	0.7	0.0	0.3	2.1	3.5*
9) *Cladopelma viridula*	6.3	7.5	2.7	10.3	3.0*

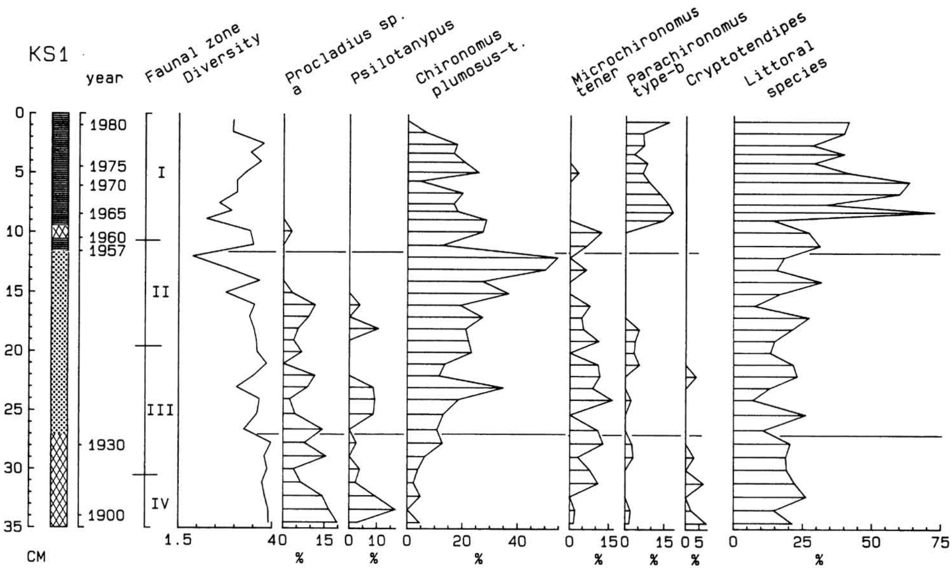

Fig. 4. The sediment sequence groups (faunal zones), subfossil faunal diversity (Shannon-index) and proportion (%) of selected taxa in the sediment samples in profile KS1. For explanation of sediment symbols see Fig. 2.

strictly shallow-water species (cf. Table 3).

Succession in the subfossil midge associations in profile KS1 can be summarized as follows. Dating and notes on the chemostratigraphy are according to Kansanen & Jaakkola (1985).

1) *Depth*: 36 to 27 cm. *Period*: about 1870 to 1930 (time scale in Figs. 2 and 4 is only approximate at these depths). *Chemostratigraphy*: No signs of temporary oxygen depletion. Zinc and dehydroabietic acid content indicate the slow beginnings of the impact of the wood-processing industry above 30 cm. Low organic content and nutrient (C, N, P) concentrations probably mean a lower productivity than in the upper parts of the core.

Fauna: The diversity of the subfossil fauna is at its highest in the core. The dominant taxa are *Procladius* sp. a, *Procladius* (*Psilotanypus*) spp. and *Cryptotendipes* spp. Their proportion decreases in the upper part of this layer, where the importance of *Chironomus plumosus*-gr. starts to increase (faunal group IV turns to III).

2) *Depth*: 27 to 11.5 cm. *Period*: about 1930 to 1957 (the upper limit is accurate). *Chemostratigraphy*: The black colour of the sediment reveals a temporary oxygen depletion. A rapid rise in the dehydroabietic acid content indicates a heavy increase of the waste water load from the wood-processing industry in the 1940s. The zinc content increase reveals the commencement of production by the fibre industry in 1943. The increase in the C-to-N ratio indicates the direct impact of the waste waters on sediments. Changes in the nutrient concentrations are small.

Fauna: The diversity of the fauna decreases upwards. This is mainly due to the strong increase in the proportion of *Chironomus plumosus*-gr. in the fauna. *Microchironomus tener* is common. *Cryptotendipes* spp. vanishes first (faunal group III) and it is followed by *Procladius* (*Psilotanypus*) spp. (faunal group II). The proportion of *Chironomus plumosus* just before 1957 is 54.5 % of the subfossil fauna. The chironomid influx has increased during the period.

3) *Depth*: 11.5 to 0 cm. *Period*: 1957-1981 (annually laminated layer). *Chemostratigraphy*: Almost permanently deoxygenated near-bottom water layers made the preservation of varves possible. Sediment chemistry (nutrients, Zn and dehydroabietic acid content) reveals a very strong industrial pollution.

Fauna: A sharp drop in the total influx of chironomids and *Chironomus plumosus*-gr. takes place in 1957. *Procladius* spp. and

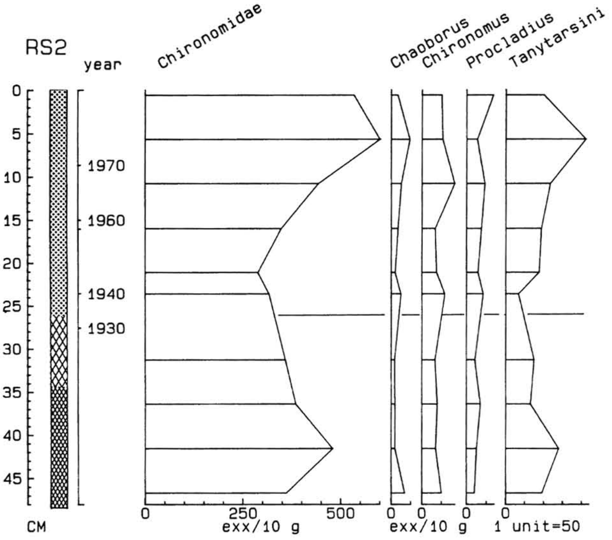

Fig. 5. The abundance (exx / 10 g d.m.) of total chironomids, *Chaoborus flavicans, Chironomus, Procladius* and Tanytarsini remains in sediment profile RS2. For explanation of sediment symbols see Fig. 2.

Microchironomus tener vanish almost totally. It is probable that abiotic conditions were too severe for the sedentary midge fauna at a depth of 10 m. Littoral species become the dominant group in the fauna (redeposition from the shallow-water area). *Parachironomus arcuatus*-gr., which has a free-swimming larva, is one of the most important species. During the latest stage of the development (after 1975) slight signs of faunal recovery can be seen (increase in the chironomid influx). The diversity in faunal group I has been variable, but lower than it has been at a depth of 15 cm.

3.2.4. Profile RS2

The 47 cm long profile RS2 from Rauttunselkä was examined by taking 10 subsamples containing 842 midge remains. The sedimentation rate has varied at this site, probably because of sediment slumping from the steep bottom gradient (Kansanen & Jaakkola 1985). Accurate estimates of sedimentation rates at various depths are not available. The time scale given in Figs. 5 and 6 is based on the C.I.C. model of ^{210}Pb distribution and gives only a rough idea of the age of the sediment layers. Sediments have also been affected by mixing.

Because estimates of sedimentation rates at various depths are inaccurate the quantitative results presented in Fig. 5 are given as exx / 10 g dry matter (cf. limitations mentioned before in conjunction with core KS1). The amount of chironomid remains per unit weight was noticeably higher than in other profiles (290-600 exx / 10 g). A high density of remains was found both at the base and in the surficial layers of the profile (Fig. 5). Changes in the number of Tanytarsini remains were similar to those in the total Chironomidae. The density of *Chaoborus, Chironomus* and *Procladius* remains appears to be rather constant throughout the entire profile.

Because possible variations in the sedimentation rate may easily lead to erroneous conclusions regarding the real abundance of the midge fauna, it is preferable to interpret the faunal changes on the basis of the qualitative composition of the subfossil fauna. The subfossil fauna of RS2 was subjected to a similar classification analysis to that applied to KS1. The result of this analysis is presented in Fig. 3. Two main groups of sediment sequences were formed: group I, 0-21.8 cm and group II, 21.8-47.4 cm. Taxa of importance in group separation are listed in Table 6.

Successive changes in the subfossil midge fauna in profile RS2 can be summarized as follows. Dating and notes on chemostratigraphy are according to Kansanen & Jaakkola (1985).

1) *Depth*: 48-26 cm. *Period*: lower layers

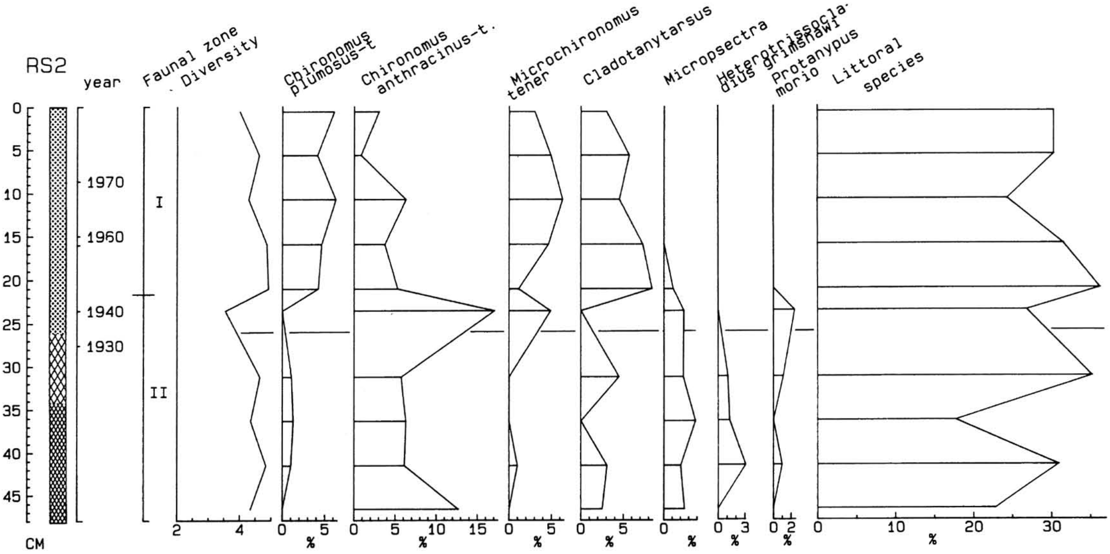

Fig. 6. The sediment sequence groups (faunal zones), subfossil faunal diversity (Shannon-index) and proportion of selected taxa in the sediment samples in profile RS2. For explanation of sediment symbols see Fig. 2.

were deposited in the 19th century. Upper limit probably represents the 1930s. *Chemostratigraphy*: No indications of temporary oxygen depletion. The high organic content, carbon and nitrogen concentrations and C-to-N ratio indicates high allocthonous organic inputs into sediments. Zinc content, at natural background level below 30 cm, starts to increase in the upper part of this layer, indicating industrial impact in this area.

Fauna: The faunal diversity is as high as it is in the surficial layers. This high diversity is due to the high proportion of the numerous littoral species in the subfossil fauna (Fig. 6). Dominant chironomid species is *Chironomus anthracinus*-gr. *Chironomus plumosus*-gr. and *Microchironomus tener* are less important, as well as *Cladotanytarsus* spp.. *Micropsectra* spp., *Heterotrissocladius grimshawi* and *Protanypus morio* are present in low numbers in all subsamples.

2) *Depth*: 26–0 cm. *Period*: The 1930s to 1979. *Chemostratigraphy*: Black sulphide layers indicate periods of oxygen depletion in the hypolimnion. The C-to-N ratio decreases, indicating eutrophication. The zinc content increases steadily due to the industrial pollution since 1943.

Fauna: *Chironomus anthracinus*-gr. reaches its maximum at 23 cm (about 1940) and then falls rapidly when *Chironomus plumosus*-gr., *Microchironomus tener* and *Cladotanytarsus* spp. become the dominant taxa. *Micropsectra* spp., *Heterotrissocladius grimshawi* and *Protanypus morio* appear to vanish completely. The proportion of the littoral species is still high and in consequence the diversity of the subfossil fauna is also high.

Table 6. Comparison of sediment sequence groups defined in Fig. 3 on subfossil taxa in profile RS2. For further explanation see text.

	Mean % of the total fauna		
Taxon cm:	Group I 0–21.8	Group II 21.8–47.4	*F* (pr.) (1.8 *df*)
1) *Micropsectra* spp.	0.2	2.6	39.4***
2) *Chironomus plumosus*-gr.	5.0	0.7	32.2***
3) *Procladius* spp.	5.3	1.6	6.7*
4) *Cladotanytarsus* spp.	5.8	2.0	6.5*
5) *Chironomus anthracinus*-gr.	3.8	9.6	6.4*
6) *Microchironomus tener*	4.0	1.2	6.3*
7) *Protanypus morio*	0.0	0.9	5.4*
8) *Heterotrissocladius grimshawi*	0.0	1.1	5.3*

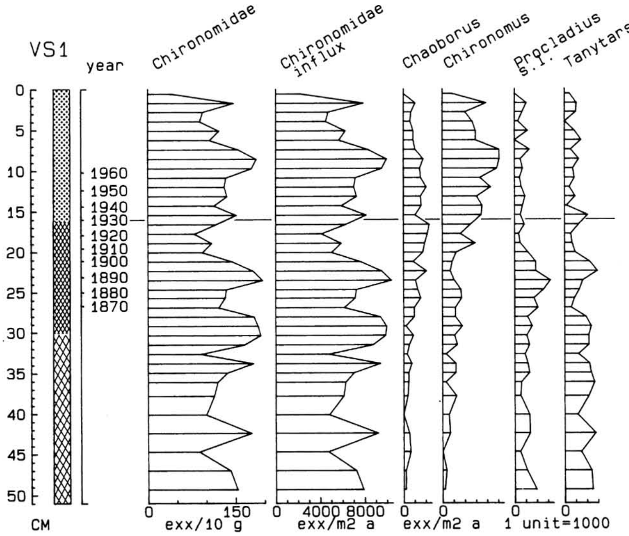

Fig. 7. The abundance (exx / 10 g d.m.) and influx (exx/m^2/year) of total chironomids, *Chaoborus flavicans*, *Chironomus*, *Procladius* and Tanytarsini remains in sediment profile VS1. For explanation of sediment symbols see Fig. 2.

3.2.5. Profile VS1

The 50.5 cm long VS1 core was examined by taking 38 subsamples containing 1633 subfossil remains. VS1 is located in the southwestern sub-basin of Vanajanselkä. The sedimentation rate has been constant in the uppermost 27 cm of the core (Kansanen & Jaakkola 1985). Thus, the data on the midge content and the influx of midge remains are the same. The time scale presented in Figures 7 and 8 represents average ages for each layer. Due to the bioturbation, the time resolution of this core is only 24.4 yr (see Kansanen & Jaakkola 1985). Below the 27 cm level the sedimentation rate is unknown. It has probably been more rapid than in the uppermost 27 cm owing to lake water level lowering (erosion material).

No remarkable trends can be seen in the total abundance of chironomid remains (Fig. 7). The chironomid remains varied irregularly between 42-97 exx / 10 g, corresponding to an influx of 2000-10 000 exx/m^2/year. The most important midge groups show, on the other hand, certain well-defined changes. The influx of *Chironomus anthracinus*-gr. increases steadily from the base of the core (0-400) towards the surface. The maximum influx (5100) can be seen at the 7 cm level, which was deposited mainly in the 1960s. Subsequently the influx decreases again. *Chaoborus flavicans* also increases steadily from the base of the core. The maximum influx of mandibles was found at the 16 cm level, which represents the 1920s (1650). The influx decreases from this maximum towards the surface. *Procladius* spp. and Tanytarsini in the lower part of the core were more abundant than in the surficial layers. The influx of both groups begins to decrease from the 22-23 cm level, which was mainly deposited during the 1890-1900 period. The maximum influx of *Procladius* was 3200 and of Tanytarsini 3000.

The result of the classification analysis of core VS1 is given in Fig. 3. Three sediment sequence groups were formed: group I, 0-20.7 cm; group II, 20.7-45.9 cm and group III, 45.9-50.5 cm. *Chironomus anthracinus*-gr. clearly constituted the most important taxon for separating these groups (Table 7). The vertical changes in the proportion of some of the taxa listed in Table 7 are presented in Fig. 8.

The succession in profile VS1, with notes on the chemostratigraphy (Kansanen & Jaakkola 1985), can be summarised as follows (Figs. 7, 8 and 9):

1) *Depth*: 50.5-30 cm. *Period*: the layer has probably been deposited during the 18th and 19th Centuries. *Chemostratigraphy*: No signs of oxygen depletion. A high organic content and the C-to-N ratio reveal high allocthonous impact. Zinc content at a natural background level. The low sedimentary chlorophyll content indicates low productivity.

Fauna: The proportion of *Chironomus*

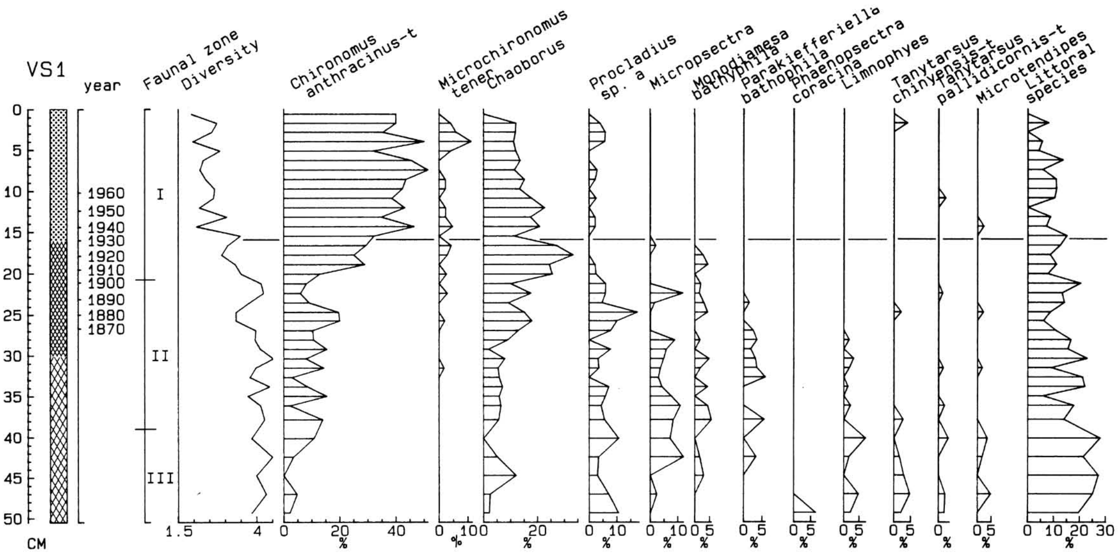

Fig. 8. The sediment sequence groups (faunal zones), subfossil faunal diversity (Shannon-index) and proportion of selected taxa in the sediment samples in profile VS1. For explanation of sediment symbols see Fig. 2.

anthracinus-gr., *Chaoborus flavicans* and *Microchironomus tener* is low. *Procladius* sp. a, *Micropsectra* spp., *Parakiefferiella bathophila* and *Monodiamesa bathyphila* are common. *Phaenopsectra (Sergentia) coracina* is present at the base of the core (faunal group III). A significant feature of the fauna is a high proportion of the shallow water species (up to 28%). This group includes *Limnophyes* spp., *Tanytarsus chinyensis*-gr., *Microtendipes* spp., *Tanytarsus pallidicornis*-gr., which are quite obviously more abundant in this layer than in the uppermost layers.

2) *Depth*: 30–16 cm. *Period*: about 1850–1930 (the limits are indefinite due to mixing; time resolution 24.4 yr). *Chemostratigraphy*:

Table 7. Comparison of sediment sequence groups defined in Fig. 3 on subfossil taxa in profile VS1. For further explanation see text.

Taxon		Mean % of the total fauna			
	cm:	Group I 0-20.7	Group II 20.7-45.9	Group III 45.9-50.5	*F* (pr.) (2.35 *df*)
1) *Chironomus anthracinus*-gr.		37.3	11.0	4.2	63.3***
2) *Limnophyes* spp.		0.0	0.7	3.2	14.6***
3) *Micropsectra* spp.		0.1	4.7	4.3	13.3***
4) *Tanytarsus chinyensis*-gr.		0.2	0.3	2.3	10.0***
5) Orthocladiinae spp.		0.0	1.1	2.3	9.3***
6) *Procladius* sp. a		1.8	5.9	7.0	9.0***
7) *Chaoborus flavicans*		16.7	9.2	4.4	8.9***
8) *Parakiefferiella bathophila*		0.0	1.9	0.7	8.3**
9) *Microchironomus tener*		2.7	0.5	0.0	8.2**
10) *Microtendipes* spp.		0.1	0.3	2.0	7.0**
11) *Monodiamesa bathyphila*		0.4	2.2	1.0	6.4**
12) *Tanytarsus pallidicornis*-gr.		0.1	0.4	1.6	5.4**
13) *Phaenopsectra (Sergentia) coracina*		0.0	0.0	1.3	3.8*
14) *Tanytarsus* spp.		1.4	1.8	4.5	3.6*
15) *Cricotopus* spp. A		2.5	5.2	4.0	3.4*
16) *Polypedilum* spp.		0.8	2.3	3.0	3.4*

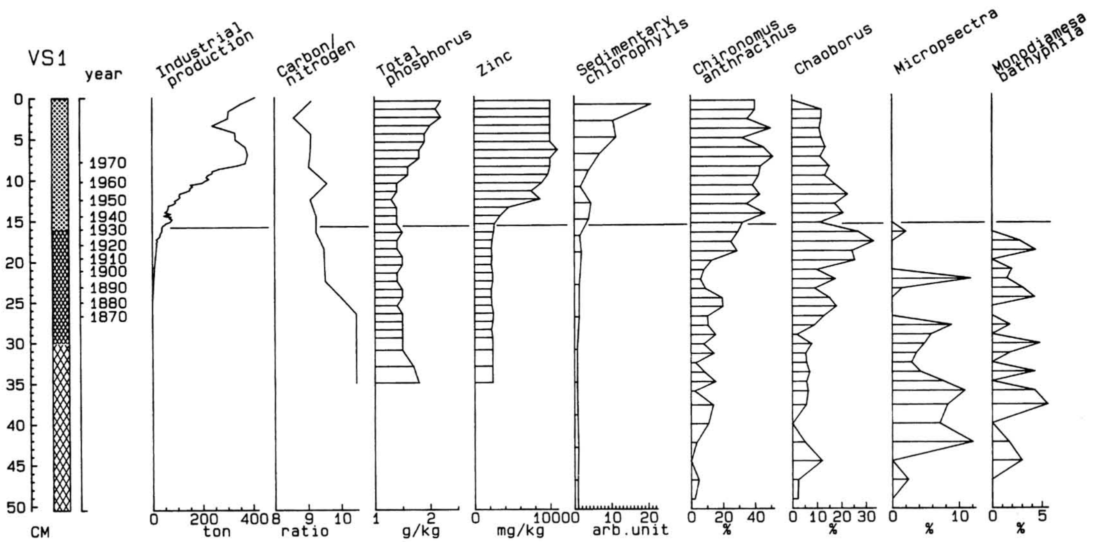

Fig. 9. Integration of selected chemostratigraphic and biostratigraphic parameters (Kansanen & Jaakkola 1985, the present study) in profile VS1. The figures for total industrial production during the period 1871-1979 in Valkeakoski are fitted to the time scale. Although these figures do not represent the total waste water load discharged to Vanajanselkä, they demonstrate the increasing trend in the waste water loading.

Oxygen conditions still favourable. The sedimentary chlorophyll content begins to increase and the C-to-N ratio to decrease, indicating eutrophication. Zinc content still at background level.

Fauna: *Chironomus anthracinus*-gr. and *Chaoborus flavicans* increase and become the dominant taxa at the beginning of the 20th Century. Due to this, the diversity of the fauna decreases rapidly. *Microchironomus tener* belongs to the progressive species. In contrast, *Procladius* sp. a, *Micropsectra* spp. and *Parakiefferiella bathophila* are clearly regressive taxa. *Monodiamesa bathyphila* is still present in low numbers. The proportion of the shallow-water species sharply decreases.

3) *Depth*: 16-0 cm. *Period*: about 1930-1979. *Chemostratigraphy*: The blackish colour of the sediment reveals temporary oxygen depletion. Sedimentary chlorophylls increase rapidly and the C-to-N ratio decreases further, indicating stronger eutrophication than lower down the profile. The total phosphorus increases steadily. The zinc content increases rapidly due to the industrial effluents occurring since 1943.

Fauna: *Chironomus anthracinus*-gr. is the dominant taxon (32-51 %). *Chaoborus flavicans* appears to become less important quantitatively speaking than at the beginning of the century. *Microchironomus tener* is present. *Procladius* sp. a is less important than lower down the core. The faunal diversity is low. *Micropsectra* spp. and *Monodiamesa bathyphila* and many shallow-water species are either absent altogether or present only sporadically.

3.2.6. *Profile VS3*

A total of 19 subsamples were taken from profile VS3 (length 48 cm), which is situated in the northeastern part of Vanajanselkä. The total amount of identified midge remains was 905. The sedimentation rate was considered by Kansanen & Jaakkola (1985) to be constant, at least in the uppermost 30 cm of the core. The time scale limitations (Figs. 10 and 11) are the same as for core VS1. Due to bioturbation, the time resolution was calculated to be 16.6 yr.

As in the case of VS1, the total amount of chironomid head capsules varies rather irregularly. The maximum influx of chironomids (20 400 exx / m^2 / year), which corresponds to 290 exx / 10 g, was found at a depth of 42 cm (Fig. 10). The influx values are generally higher than in core VS1. The most abundant chironomid taxon, *Chironomus anthracinus*-gr., becomes far more important

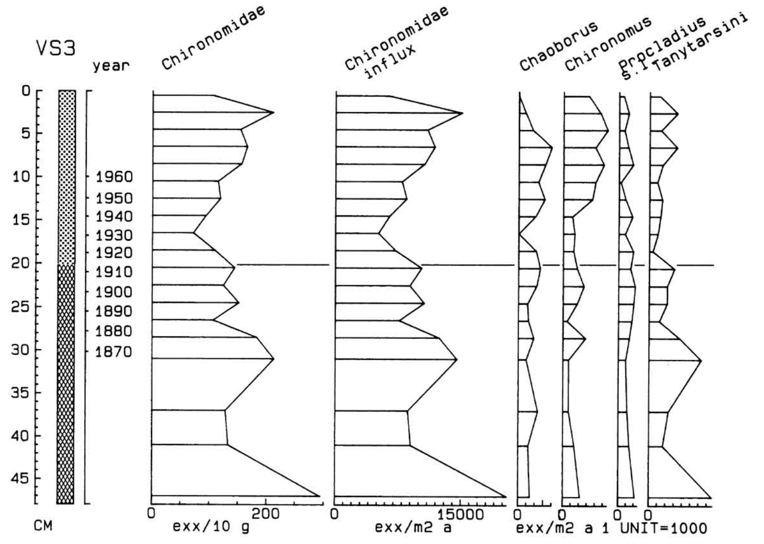

Fig. 10. The abundance (exx / 10 g d.m.) and influx (exx/m^2/year) of total chironomids, influx of *Chaoborus flavicans, Chironomus, Procladius* and Tanytarsini remains in sediment profile VS3. For explanation of sediment symbols see Fig. 2.

in the uppermost 14 cm than lower down the core (max. 5500). *Chaoborus flavicans* also has high influx values in the uppermost 14 cm, but the trend is not very clear. *Procladius* spp. shows no great variations in the profile. On the other hand Tanytarsini are clearly more abundant below 20 cm than in the uppermost layers.

Respecting the classification of the sediment sequences (Fig. 3) two groups emerged: group I, 0–15 cm and group II, 15–48 cm. The characteristic taxa for each group are listed in Table 8. The total number of taxa, which show clear vertical changes in the core, is smaller than in core VS1.

The faunal changes in VS3 can be summarized as follows:

1) *Depth*: 48–20 cm. *Period*: the lower layers were probably deposited in the 18th Century, while the upper limit represents the 1910s. *Chemostratigraphy*: Oxygen conditions have been favourable. The high C-to-N ratio reveals

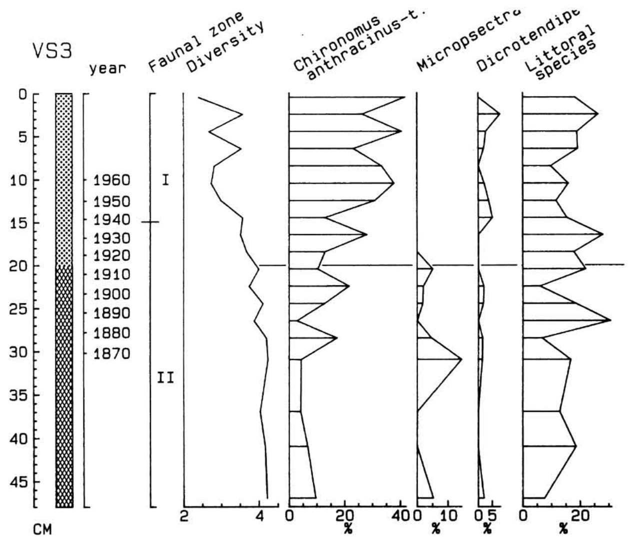

Fig. 11. The sediment sequence groups (faunal zones), subfossil faunal diversity (Shannon-index) and proportion of selected taxa in the sediment samples in profile VS3. For explanation of sediment symbols see Fig. 2.

Table 8. Comparison of sediment sequence groups defined in Fig. 3 on subfossil taxa in profile VS3. For further explanation see text.

Taxon	Mean % of the total fauna		
	Group I	Group II	*F* (pr.)
cm:	0-15	15-48	(1.17 *df*)
1) *Tanytarsus* spp.	0.7	5.7	51.5***
2) *Chironomus anthracinus*-gr.	30.8	11.8	20.5***
3) Orthocladiinae spp.	0.0	2.9	8.7**
4) *Chironomus* spp.	0.0	1.5	7.2**
5) *Micropsectra* spp.	0.0	3.0	6.5*
6) *Dicrotendipes* spp.	2.9	0.8	6.5*

high allochtonous inputs of organic matter. The zinc content is at the natural background level.

Fauna: Although *Chironomus anthracinus*-gr. is the dominant taxon, its proportion is markedly lower than in the upper part of the core (Fig. 11). *Micropsectra* spp. and *Tanytarsus* spp. make a more important contribution to the fauna than they do in the uppermost layers. The faunal diversity is high. The proportion of shallow-water species varies between 6.6-22%.

2) *Depth*: 20-0 cm. Period: about 1915 to 1979. *Chemostratigraphy*: The sediment colour gradually turns to blackish, which indicates temporary periods of oxygen depletion. The C-to-N ratio decreases towards the sediment surface, revealing eutrophication. The organic content, carbon, nitrogen and phosphorus contents increase steadily towards the sediment surface. The zinc content begins to increase at about 12-14 cm, which reveals the direct impact of industrial effluents in the 1950s.

Fauna: *Chironomus anthracinus*-gr. increases especially in the 1940s and its proportion in the total subfossil fauna reaches the 23-42% level in the uppermost 12 cm. *Micropsectra* spp. vanishes completely from the fauna in the 1920s. The importance of *Tanytarsus* spp. also decreases sharply. *Dicrotendipes* spp. appear to become more important than they are below 20 cm. The proportion of the shallow-water fauna varies between 10-28%. In contrast to profile VS1 there is no significant vertical change in this respect in profile VS3, but the variations are more irregular. The diversity of the fauna decreases clearly (the trend is similar to that in profile VS1).

4. Discussion

4.1. Information value of the subfossil midge fauna

The crucial problem in the interpretation of the observed changes in the subfossil midge fauna is knowing what relationship exists between the subfossil midge assemblage at a certain depth in the core and the fauna that once lived in the same place. There are a number of factors which should be taken into account (cf. excellent discussion of Hofmann 1971a, 1971b):

1. One of the most important factors is the influence of the redeposition of midge remains from shallow erosion and transportation bottoms on deep accumulation bottoms (cf. Kansanen & Jaakkola 1985). According to the terminology used by Hofmann (1971a,b), it can be said that subfossil assemblages in profundal cores are hardly ever pure necrocoenoses (fossil communities formed and deposited in the same biotope). Rather, they are thanatocoenoses, which include faunal elements secondarily transported to the thanatope (corresponds to biotope) and mixed with the original necrocoenose.

2. Chironomids and *Chaoborus* spp. pass through four larval stages before they pupate. Theoretically, if the larval mortality is not taken into account, the number of chironomid head capsules found in the sediment should be divided by four in order to obtain a comparative abundance estimate with the corresponding live fauna. In the case of *Chaoborus* each mandible pair represents one larval instar, which means dividing by eight. In practice the situation is complicated. Due to bacterial decomposition or mechanical stress, e.g. during transportation in the lake bottom, tiny and weakly sclerotized head capsules of the first chironomid instar (larvula) are always lost (Stahl 1959, Hofmann 1971a). It is also obvious that part of the second instar head capsules may be lost during sieving, at least if they are partly broken. In order to avoid sieving losses, a sieve mesh of 100 μm was used in the present study (Stahl 1959 125 μm, Hofmann 1971a 132 μm). In the case of *Chaoborus* larvae all first and second instar mandibles are also broken or lost during sieving (Stahl 1959). The observations made in

the present study showed that the majority of mandibles belonged to the fourth instar. The sieve used is not quantitative for the third instar mandibles (cf. Stahl 1959). If the third instar mandibles are preserved paired, they have a better chance of being retained in the sieve than single mandibles.

3. It is known that in some chironomid species the head capsule of the fourth instar often sticks in the pupa and therefore the proportion of the species in the thanatocoenose may be underestimated. According to the observations from the emergence traps made in the present study, this phenomenon sometimes takes place in the case of *Chironomus* larvae, but is very rare in other taxa. More significant may be the fact that chironomid species have different life cycles. The total number of head capsules produced per year is different, depending on whether or not the species has one or two generations per year or has a two-year life cycle (Hofmann 1971a). Species having two-year life cycles are naturally underestimated in the thanatocoenose in comparison to species having a one-year cycle or several generations per year. It is known that *Chironomus anthracinus* may even have larvae with two-year life cycles and one-year cycles in the same lake (Jonasson 1969). *Chironomus plumosus* may have one or several generations a year in the same lake in different depth zones (Brundin 1949). From the palaeolimnological point of view it is significant whether or not the same species may change its life cycle during the period of interest. It is known that this kind of change may take place due to climatic changes over long periods of time (Hofmann 1971a). In the present study, however, such changes seem to be unlikely because of the short period considered in the lake history.

For the reasons given above it is clear that estimates of population densities based on the thanatocoenose have to be considered as being merely tentative. Estimates of influx of a species (exx / m^2 / year) in the profile are, however, valuable, because they suggest changes in the abundance of this species during the lake development. The palaeolimnological interpretations of the successions in the midge fauna are usually made on the basis of the faunal composition at various depths of the profile (e.g. Stahl 1959, Hofmann 1971a, Warwick 1980). If the preservation of the remains of a species occurs uniformly in the thanatocoenosis during the whole period of interest, its proportion is dependent on its original abundance in the biocoenose, and the composition of the thanatocoenose can be used to describe the structure of the original midge community.

When the composition of the thanatocoenose and the corresponding live midge community estimated by a standard zoobenthos technique is compared (Table 4), one should take into account that the subfossil faunal composition represents a composite of the whole year. Ekman-Birge samples were taken in late summer. There are some midge species emerging in spring whose larvae in August are too small to be retained in the 0.6 mm sieve used. The sieving losses are naturally higher when using a 0.6 mm sieve than when a 0.1 mm sieve is employed.

The differences between palaeolimnological and zoobenthic methods only partly explain, however, the significant differences between the composition of the subfossil and live faunas given in Table 4. These results indicate that redeposition of shallow-water fauna is an important factor affecting the composition of thanatocoenoses in the profiles of Lake Vanajavesi. The most convincing evidence of the redeposition can be seen in the uppermost layers of profile KS1 (Table 4). The macrozoobenthos investigations of Kansanen & Aho (1981) showed that in August 1965 and 1971 the northern basin of Kärjenniemenselkä (KS1) was empty of macrozoobenthos below a 5 m depth and unsuitable for all higher forms of life. The meiozoobenthos study (100 μm sieve) verified this observation (Kansanen 1981). In 1977 only a few larvae of *Chironomus plumosus* and *Tanytarsus* sp. were found. The sediment has been annually laminated since 1957, which also reflects a lack of benthic activity (Kansanen & Jaakkola 1985). Despite this, a diverse subfossil fauna was found in the layers deposited in the period 1971-1981. The high proportion of the shallow-water species also reveals the littoral origin of the thanatocoenose.

The taxa which are restricted to the littoral zone, often in association with aquatic plants or species having planktonic larvae (e.g. *Parachironomus* spp.), are usually easy to separate from the deepwater fauna (cf. Table 3; Hofmann 1971a, Warwick 1980). It is more difficult to evaluate what the significance of redeposition is in the case of eurybathic species occurring at a wide range of depths. Among the species which are abundant in the profundal zone of Vanajavesi (cf. Table 1) are *Chironomus* spp., especially *C. plumosus* (*C. anthracinus* and *C. neocorax* prefer deepwater area), *Procladius* sp., *Cladopelma viridula*, *Cryptochironomus* spp., *Microchironomus tener* and many *Tanytarsus* spp. In profile KS1 most of the *Chironomus plumosus* head capsules found in the uppermost 11.5 cm must have been redeposited from the littoral zone, where this species was very abundant during the period 1965-1977 (Kansanen & Aho 1981). The difficulty of separating species of the genus *Tanytarsus* makes it almost impossible to evaluate the significance of redeposition. *Tanytarsus pallidicornis*-gr. and *T. chinyensis*-gr. are littoral taxa (cf. Hofmann 1971a).

The profundal origin is easy to detect in the case of members of the *Tanytarsus lugens* community (Brundin 1956). These species are known to be mostly cold-stenothermal, polyoxybiontic species occurring in the profundal zone of deep, stratified lakes. Of these species only a few were found in Lake Vanajavesi, because the thermal stratification is labile. *Phaenopsectra* (*Sergentia*) *coracina*, *Protanypus morio*, *Monodiamesa bathyphila* belong to this profundal group, although the last mentioned species is also able to live in low numbers in the sublittoral zone at higher temperatures. The most abundant of this group of species has been *Micropsectra* spp.. According to Säwedal (1982), there are seven species occurring in lakes, four of them exclusively in the profundal zone, but three species in the littoral zone as well. Although it was impossible to identify the larval head capsules to the species level, it is obvious that *Micropsectra* spp. is a profundal element in the subfossil fauna. This view is supported by the fact that *Micropsectra* were present in profiles VS1, VS3 and RS2, which are deepwater sites (depth 19-21 m), but not a single specimen in profile KS1, which belongs to the lower sublittoral zone (10 m). The two hypopygia identified belonged to *M. insignilobus* or *lindebergi* (Säwedal, pers. comm.), which are strictly profundal species.

The significance of the redeposition of midge remains in the four profiles can be evaluated on the basis of the proportion of the shallow-water species (Table 4) and also from the total abundance and influx values (Table 9). Besides in profile KS1, which was discussed earlier, redeposition seems to be very significant in profile RS2. Comparing the chironomid influx value of 68 000 with the abundance of live fauna (100-300) shows that most of the thanatocoenose originates from the upper bottoms. This is in accordance with the observations of Kansanen & Jaakkola (1985), who stated that sediment slumping has taken place at site RS2 from the steep bottom gradient between the deeps and the shore (13 %). In large Vanajanselkä the significance of redeposition is less than in KS1 and RS2, but it is not, however, negligible. The thanatocoenose of VS1 seems to be most representative of the profundal fauna. The proportion of the shallow-water taxa is small and the influx estimates are of the same order as the measured densities of the live chironomid fauna. If the influx is divided by three (cf. Hofmann 1971a), the chironomid deposition at site VS1 in the 1970s was about 1700 exx / m^2/year (cf. 1000-3000 ind/m^2, Table 9).

Table 9. The average number of chironomid head capsules per 10 g of dry sediment, average chironomid influx (exx/m^2/year) and proportion of littoral taxa in the 0-6 cm layer of the four profiles. Sedimentation rates used in the influx calculations are according to Kansanen & Jaakkola (1985). In the case of RS2 a value of 120 mg/cm^2/year was used, which is based on ^{210}Pb dating. The abundance (ind/m^2) of chironomids, as measured in August 1971 and 1977 using a 0.6 mm sieve, is also indicated (min. and max. abundance).

	KS1	RS2	VS1	VS3
exx / 10 g d.m.	160.4	566.7	98.7	156.6
exx/m^2/year	12 307	67 998	5120	10 769
littoral- %	41.6	36.6	6.5	23.4
ind/m^2 (live fauna)	0-74	99-320	1139-2863	1306-1875

Some previous authors have paid attention to the significance of redeposition. Wiederholm (1979), working on Lake Washington found that more than 80 % of the total subfossil fauna in a core taken from a 63 m depth near the shore originated from a shallow-water area. According to Hofmann (1971a), the allocthonous part of the thanatocoenose in the profundal of the Grosser Plöner See was dominant in the surficial layers. On the other hand, many authors have considered the influence of redeposition to be negligible (e.g. Carter 1977, Wiederholm & Eriksson 1979, Warwick 1980).

In conclusion, it seems obvious that redeposition of the shallow-water fauna on the profundal bottoms may be the most significant factor disturbing palaeolimnological interpretation of the midge thanatocoenoses. The extent of this phenomenon depends on the dynamic conditions of the bottom in the vicinity of the sampling site. It is particularly important in the depths near the shore, where even slumping of the sediment may take place. In complex lake basins such as Vanajanselkä the large area of erosion and transportation bottoms and complex currents may cause significant amounts of remains to be redeposited from accumulation bottoms far from shore. Detailed identification of the midge remains and comparison of the ecology and bathymetric distribution of the species are the only means of avoiding misinterpretation of the thanatocoenoses affected by redeposition.

Another difficulty in interpreting the stratigraphy of subfossil midge remains is the fact that the time resolution is reduced in the profiles where an abundant bottom fauna is present. In some cases the mixing layer can be very thick. The large bodied larvae of *Chironomus plumosus*-gr. have been observed to mix sediment in some shallow lakes to a depth of 15-40 cm (Frank 1982, Dévai & Moldován 1983). The rearrangement of head capsules in the mixing layer is due not only to the physical mixing, but also to the moulting of larval instars below the sediment surface. An attempt was made by Kansanen & Jaakkola (1985) to take the disturbing effect of bioturbation into account in the dating of the profiles from Vanajavesi. The results support the view that the thickness of the mixing layers was notably smaller than in the studies of Frank (1982) and Dévai & Moldován (1983).

4.2. Succession in the midge communities of Lake Vanajavesi

According to Järnefelt (1929), the profundal zoobenthos of Vanajanselkä was dominated in August 1926 by an amphipod, *Pontoporeia affinis* Lindström (49.8 %). The midge fauna was sparse (an average of 35.6 ind/m^2). *Monodiamesa bathyphila* (53.1 %) and *Tanypus* spp. (probably *Procladius* spp., 46.9 %) were the only taxa. In the sublittoral the midge abundance was also low (22.4 ind/m^2). The sublittoral taxa were *Chaoborus* (sub *Sayomyia*), *Cryptochironomus* spp. and *Tanypus* spp.

According to Kansanen & Aho (1981), the zoobenthos in Vanajanselkä changed drastically during the period 1926-1965. *Pontoporeia affinis* decreased in the profundal and became more abundant in the sublittoral. The abundance and biomass of the total zoobenthos was markedly higher than in 1926. This increase was mainly due to midge larvae. The midge fauna was characterized by a high dominance of *Chironomus* spp. (97 %). The population density of *C. anthracinus* in 1965 was 2025 ind/m^2. Other species were *C. neocorax* and, in low numbers, *C. plumosus*. *Procladius* spp. were also present in the profundal zone. On the other hand, *Monodiamesa bathyphila* almost completely vanished, although it was found commonly in the sublittoral.

Later (1971, 1974, 1977) eutrophication and pollution in Vanajanselkä progressed and *Pontoporeia affinis* vanished almost totally from the profundal as well as from the sublittoral. A drift towards a *Chironomus plumosus* community, which was present in Rauttunselkä, was noted in Vanajanselkä in 1977. *Monodiamesa* vanished almost totally from the sublittoral. The abundance and dominance of *C. anthracinus* decreased.

Chaoborus larvae appeared to be more abundant during the period 1965-1977 (max. 700 ind/m^2) than in 1926 (max. 86 ind/m^2). This change must be interpreted with certain reservations, as the sampling method is not necessary quantitative due to the semipelagic way of life of *Chaoborus* larvae (Kansanen & Aho 1981).

The background data presented above is very useful when interpreting the succession in the thanatocoenoses of profiles VS1 and VS3. Profile VS1 reflects the profundal succession better than VS3, because the impact of littoral redeposition is significantly smaller. The number of subsamples was higher in VS1 than in VS3. Both profiles confirm the strong increase in abundance of *Chironomus anthracinus*-gr. in Vanajanselkä. This taxon includes two species with a preference for profundal bottoms: *C. anthracinus* and *C. neocorax*. Their ecology is quite similar in relation to the water quality, although *C. neocorax* probably has lower nutritional requirements and a better tolerance to oxygen lack than *C. anthracinus* (Kansanen et al. 1984). Their separation from the subfossil material was only possible in the case of complete fourth instar head capsules. The results indicate that no significant change in their proportions has taken place in Vanajanselkä during this century. Of the other changes that can be interpreted as profundal successions, one of the most significant is the disappearance of *Micropsectra* spp., which was an important taxon, especially in the preindustrial layers in both profiles. The trend presented by Kansanen & Aho (1981) in the case of *Monodiamesa bathyphila* is confirmed by profile VS1. However, this species has never been dominant in the profundal fauna of Vanajanselkä. *Procladius* spp., especially *Procladius* sp. a, seems to have been suppressed in the profundal fauna as the dominance of *Chironomus* spp. increased. *Microchironomus tener* probably inhabitated the profundal zone of Vanajanselkä when the *Chironomus* spp. became dominant. *Phaenopsectra* (*Sergentia*) *coracina*, on the other hand, was present in the profundal only in the preindustrial era. *Chaoborus flavicans*, which is known to prefer hypolimnetic water layers with a low oxygen concentration and a high humus content (Hofmann 1971a), seems to have increased up to the first decades of this century. Since then no increase has taken place. It cannot be confidently stated that the other taxa are correlated with profundal changes, because most of them belong to the littoral elements.

To summarise, the profundal zone of Vanajanselkä was characterised in the 19th century and at the beginning of the 20th century by a diverse midge association, which can be designated partly according to Järnefelt (1929, 1953) as a *Micropsectra* - *Monodiamesa* community. Table 10 suggests its composition. It should be noted that both *Chironomus anthracinus* and *C. neocorax* are among the most abundant species of this community. In the first decades of this century the *Micropsectra* - *Monodiamesa* community was replaced by the present monotonous *Chironomus anthracinus* community. The accurate dating of this change is difficult to determine, because the stratigraphic limits in the profiles are diffuse due to bioturbation (cf. Kansanen & Jaakkola 1985). Both profiles of Vanajanselkä indicate that the disappearance of the *Micropsectra* - *Monodiamesa* type of community has taken place gradually during the period 1910-1930.

It is clear that Järnefelt's (1929) study does not give an entirely truthful picture of the abundance and composition of the midge fauna in Vanajanselkä. It was based on one sampling in August and for this a coarse sieve (0.7-0.8 mm) was used. It is probable that *Chironomus* (and other) larvae were not large enough at that time to be retained by the sieve. The development of these larvae was probably slower under lower nutrient conditions than at the present time, when the third instar develops by the end of July (*C. anthracinus* and *C. neocorax*) (cf. Jonasson 1969). The sieve used by Järnefelt (1929) systematically lost all Tanytarsini, which have small head capsules even in the fourth instar (width 0.5 mm, Brundin 1951). The stratigraphic results indicate that in fact no dramatic growth in the total abundance of midge larvae has taken place in Vanajanselkä during this century. Significant changes in the proportions of the various size classes have occurred. The high increase in the numbers of large *Chironomus* larvae probably means that the biomass of the midge benthos has increased, indicating an improvement in the general production level of the lake.

Table 10. The main components of the subfossil fauna in faunal zone II (20.7-45.9 cm, Fig. 7) of profile VS1, which layer represents a *Micropsectra* - *Monodiamesa* type community.

Taxon	%
1. *Procladius* spp. (incl. spp. a, c, d)	22.0
2. *Chironomus anthracinus*-gr. (incl. *anthracinus* and *neocorax*)	14.4
3. *Tanytarsus* spp.	9.5
4. *Micropsectra* spp. (incl. *M. insignilobus* or *lindebergi*)	6.4
5. *Polypedilum* spp.	4.4
6. *Monodiamesa bathyphila*	3.1
7. *Harnischia curtilamellata*	2.7
8. *Parakiefferiella bathophila*	2.2
9. Pentaneurini spp.	2.2
Littoral taxa	19.6
Other taxa	13.5
Total	100.0

Changes in the proportion and composition of the littoral faunal component in the thanatocoenose may also be indicative of the general state of the lake. The proportion of littoral species in, for example, profile VS1, is noticeably higher below the 30 cm level than it is in the upper layers (Fig. 8). This may partly be due to the favourable oxygen conditions in the whole water column which made it possible for the generally polyoxybiotic shallow-water fauna to live deeper than in the present Vanajanselkä, where the oxygen lack

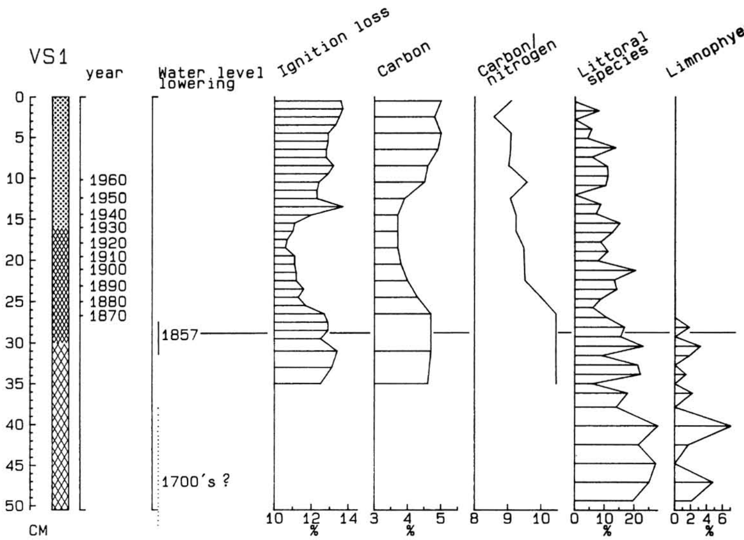

Fig. 12. Integration of selected chemostratigraphic and biostratigraphic parameters with the artificial water level lowering made in the 18th Century and again in 1857. Time scale not reliable below 27 cm.

greatly limits the number of species in the profundal zone (cf. Brundin 1949). The high proportion of *Limnophyes* spp. below 30 cm and its absence from the upper layers of VS1 is, however, difficult to explain on these grounds. *Limnophyes* spp. (cf. *prolongatus*) in lakes form part of the terrestrial fauna of the moist biotopes on the shoreline (Brundin 1949). To a lesser extent they may live in the littoral zone, but although adults were common on the shoreline Brundin (1949) found no specimens from lake bottom samples in his extensive study.

The probable reason for the above phenomenon is the artificial lowering of water levels during the 18th and 19th Centuries (Fig. 12). The most significant, and final, lowering operation was carried out in 1857, when the water level was lowered by 2 m (cf. Kansanen & Jaakkola 1985). Owing to these operations broad zones of clayey alluvial bottom were exposed and a large amount of surface material was washed back into the lake before the soil became bound by the invading vegetation (Auer 1924, Vuorela 1980). The bottom dynamic conditions in the lake changed. Part of the accumulation bottoms was exposed to erosion. It is obvious that the sediment layers below 25 cm contain erosion material having a high organic content, high C-to-N ratio and high proportion of littoral chironomids in profile VS1 (Fig. 12). Vuorela (1980) noted the same phenomenon in her pollen studies of cores taken from the littoral of Vanajanselkä. In the sediment layers containing erosion material the chronological order in the sediment profile was disturbed and impossible to date using the ^{14}C-method. This means that these layers may contain midge remains from much older periods of the lake history than the 19th Century. It was observed that the proportion of fragmented head capsules was high below the 25 cm level in both profiles VS1 and VS3.

The results presented in Fig. 12 demonstrate that subfossil chironomid analysis is valuable not only from the typological point of view, but also as an indicator of past water level changes in the lake basin. It is suggested that the ratio of the littoral chironomids to the strictly profundal chironomids can be used as an index of water level changes in a similar way to the planktonic - littoral ratio based on the relationship between *Bosmina* and chydorids (Alhonen 1970). The use of such an index involves detailed identification of the subfossil fauna.

There is no background data available on the zoobenthos of Kärjenniemenselkä and Rauttunselkä prior to 1965. In the period 1965–1977 Rauttunselkä was inhabited by a *Chironomus plumosus* community characterised by *Procladius* sp. c and *Microchironomus tener* (Kansanen et al. 1984). *Chironomus anthracinus* and *C. neocorax* were also present in low numbers. Although profile RS2 is more indicative, in fact, of conditions in the shallow-water area than in the deep, some conclusions on the profundal succession can still be made. The qualitative composition of the thanatocoenose at the base of the core reveals that a *Micropsectra - Monodiamesa* community similar to that of Vanajanselkä was also present in Rauttunselkä. *Chironomus anthracinus*-gr. and *Micropsectra* were characteristic profundal elements in the fauna. *Heterotrissocladius grimshawi* and *Protanypus morio* were present in low numbers. Possibly during the period 1930-1940 the proportion of *Chironomus anthracinus*-gr. began to increase and *Micropsectra* spp. and other oligotrophic species vanished. The period of existence of the *Chironomus anthracinus* community in Rauttunselkä was brief. The present *C. plumosus* community had probably replaced it by the 1940s.

The succession in Kärjenniemenselkä is not entirely compatible with that observed in Vanajanselkä and Rauttunselkä. The basin of Kärjenniemenselkä is shallow and the depth of KS1, 10 m, represents a lower sublittoral zone (sensu Eggleton 1932). Hence, the profundal components of the fauna (e.g. *Chironomus anthracinus*-gr., *Micropsectra* spp., *Phaenopsectra* (*Sergentia*) *coracina* and *Protanypus morio*), which were common in profiles VS1, VS3 and RS2, are absent or scarce here. The sublittoral community present in the preindustrial era can be termed a *Procladius - Cryptotendipes* association. It was gradually replaced by a *Chironomus plumosus* community (with *Microchironomus tener*). This succession was correlated with a high increase in the chironomid influx. In the latest stage of development the sedentary fauna disappears from the depths of Kärjenniemenselkä. During this stage (1957-1981) the thanatocoenose mainly reflects conditions in the littoral zone. Kansanen & Aho (1981) reported that the abiotic conditions improved drastically in 1977 in the littoral zone due to the fall-off in waste water loading. Chironomid larvae were found in low numbers even in the depths of Kärjenniemenselkä. This improvement is apparent in the annually laminated sediment layers of KS1 after 1975. The chironomid influx began to rise sharply as a result of faunal recovery in the littoral zone. The preservation of the laminated structure in the uppermost layers shows that the deep bottom was mostly devoid of bottom animals even during this period of recovery.

4.3. Ecological significance of the observed succession

The succession in the profundal midge communities in Lake Vanajavesi seems to have passed through the following stages during the 19th and 20th Centuries:

I *Micropsectra - Monodiamesa* community.

II *Chironomus anthracinus* community.

III *Chironomus plumosus* community.

IV Disappearance of profundal midge fauna (*Chironomus plumosus* community restricted to the shallow-water zone).

What is the relationship between these communities and the general state of the lake ecosystem? According to Brundin (1949, 1951, 1956), the annual minimum oxygen concentration is the primary factor controlling the succession in profundal chironomid communities. The availability of food becomes limiting only in ultraoligotrophic lakes. This differs from the statements made by Warwick (1975), Saether (1979) and Wiederholm (1980). According to them, the availability of food is the governing mechanism. The results of Kansanen et al. (1984) supported this view. Lack of oxygen appears to be a critical factor only in lakes of advanced eutrophy, or in lakes where the oxygen level for other reasons is particularly low due, for example, to a high humus load or a hypolimnion of low volume. Warwick (1980) paid attention to the significance of sedimentation processes, which can modify the effect of food availability on the profundal chironomid communities. Highly increased mineral sediment accumulation caused a drift towards an oligotrophic fauna in the Bay of Quinte, Lake Ontario. The supply of food materials in the sediments was reduced through dilution. The freshly sedimented food materials were also buried intact and remained unavailable to the chironomid community. It is also probable that highly increased inputs of erosion materials to the lake caused turbidity in the trophogenic layer and therefore a decrease in the primary production level (Warwick 1980). Whatever the cause, the role of sedimentation processes must be carefully evaluated when successions in midge communities are interpreted.

The *Micropsectra - Monodiamesa* community of Vanajavesi has no counterpart in the lake typology of Brundin (1956). This is mainly due to the fact that the lake does not stratify regularly. Long periods of summer stagnation may be interrupted by strong winds, when the bottom temperatures rise and the oxygen reserves of the hypolimnion are improved. Due to high bottom temperatures (generally 14–15°C) in late summer, the strictly cold-stenothermal components of the *Tanytarsus lugens* community are lacking. The faunal composition resembles that of the unstably stratified oligotrophic lakes studies by Brundin (1949). Typical of these lakes (e.g. Lake Innaren) is the presence of some less cold-stenothermal members of the *Tanytarsus lugens* community, together with a diverse *Tanytarsus, Procladius, Chironomus* (both *C. plumosus* and *C. anthracinus*), *Stempellina* and *Stempellinella* fauna. *Micropsectra insignilobus* and *M. lindebergi* are polyoxybiontic, cold-stenothermal species (Säwedal 1982). It is, however, obvious that they can tolerate relatively high temperatures. Both species are found in Lake Puruvesi, an oligotrophic lake in eastern Finland, from areas where the thermal stratification is labile (Säwedal 1976, Lindeberg, pers. comm.).

The stratigraphic results (C-to-N ratio, sedimentary chlorophylls, faunal composition) indicate that the productivity was at one time significantly lower than it is today. It is most likely that the improvement of the food availability was the main reason for the change from a *Micropsectra - Monodiamesa* community to a *Chironomus anthracinus* community. This change had already commenced in Vanajanselkä when the FeS-coloured gyttja began to occur in profiles VS1 and VS3.

Maristo (1941) included Lake Vanajavesi on his map of the regional distribution of the dominant floristic lake types in the eutrophic, southern area. Järnefelt (1956) assigned Lake Vanajavesi to the chthonio-eutrophic lake type on the basis of the composition of the planktonic flora. The stratigraphic results of Auer (1924) indicate that Lake Vanajavesi earlier in its post-glacial history was a 'gyttja-lake' and became a 'dy-gyttja lake' due to the deterioration of the climatic conditions. Under the influence of allochtonous acid humus material, which bound the original nutrient reserves of the water, the lake changed course towards dysoligotrophy. This kind of phenomenon has been reported in many lakes in Finland (Vasari 1962, Alhonen 1967, Tolonen 1967, Kukkonen & Tynni 1970, Kukkonen 1973, Huttunen & Tolonen 1977). In Lake Vanajavesi the dysoligotrophication was probably strengthened by the fact that large areas of peat bogs were left below the water level because of transgression induced by land upheaval (Auer 1924). Preliminary analyses of a 3 m long core taken from Vanajanselkä showed that at the base of the core the chironomid fauna was dominated by *Chironomus* fauna typical of eutrophic lakes (Kansanen, unpublished). What role the artificial water level lowering during the 18th and 19th Centuries played remains an open question. It is possible that increased turbidity has directly affected the primary production, and also the zoobenthos by reducing the food availability as described by Warwick (1980). In fact, a *Micropsectra* fauna, together with *Harnischia curtilamellata* and *Heterotrissocladius*, is reported as being typical of lakes receiving allothonous mineral sediments (Pagast 1943, Reiss 1968, Warwick 1980).

Kansanen & Aho (1981) and Kansanen et al. (1984) discussed in detail the relationship between the trophic status of the lake and community types II–IV. The *Chironomus* communities conform very well to the lake typology of Brundin (1956). This is due to the fact that members of these communities are eurythermal. The development of a *Chironomus* community in Lake Vanajavesi was dependent on the increase of the nutritional value of the bottom sediments. The main factor controlling succession from a *C. anthracinus* community towards a *C. plumosus* community and finally towards the disappearance of the profundal fauna appears to be the oxygen content of the water (Kansanen & Aho 1981). The trophic differences between Vanajanselkä, Rauttunselkä and Kärjenniemenselkä were small. The main difference in the water quality between these areas in 1965–1977 was the annual minimum oxygen concentration: 18 % in the *C. anthracinus* area, 4 % in the *C. plumosus* area, and about 0 % in Kärjenniemenselkä with a depauperate profundal (averages during the period 1970–1977 at 15 m). The oxygen content of the hypolimnion naturally depends on the trophic status, but several factors modify this relationship. The main reason for the low oxygen status in Kärjenniemenselkä and Rauttunselkä was a direct effect of the industrial waste waters having a very high biological oxygen demand.

Recently more attention than has been the case in traditional limnological literature has been paid to the significance of altered predator - prey interactions in the eutrophication successions (cf. Stenson 1972, Nilssen 1978, Henriksson et al. 1980). It is obvious that selective predation may be a significant factor modifying successions in pelagic systems (zooplankton) and probably also in the littoral zoobenthos. In the case of the profundal zoobenthos, which is less important as fish food than the littoral benthos, the possibility of selective predation is probably limited to the short period of emergence, at which time fishes effectively consume pupae rising from the bottom to the surface (Grimås 1963). It has been shown that tube-dwelling chironomid species are not effectively predated by trouts from the lake bottom (Brown et al. 1979). The predation is more or less random in the case of fishes taking their food mainly from bottom mud (see Healey 1984). It therefore seems unlikely that altered predator - prey interactions would have significantly modified the observed successions on profundal bottoms, but rather that these successions are directly regulated by the availability of food and the oxygen content of the water.

4.4. Main features of the pollution history of Lake Vanajavesi

The chemostratigraphic (Kansanen & Jaakkola 1985) and biostratigraphic evidence of the limnological development of Lake Vanajavesi are integrated with the socio-economic history of the surrounding area in the following brief summary (cf. Fig. 9 and Table 11). The trends are in most cases clear, but because the stratigraphic limits in the profiles are mainly diffuse due to bioturbation, plotting the limnological changes on the historical time scale may in some cases prove difficult. It is clear that more palaeolimnological analyses, especially diatom and cladoceran analyses, are needed, before all details of the eutrophication and pollution development can be fully understood.

Table 11. Integration of some significant stratigraphic sediment parameters with the midge community type in the four profiles. Carbon-to-nitrogen ratio, sedimentary chlorophyll content (arbitrary units) and zinc content (mg/kg) are according to Kansanen & Jaakkola (1985).

	KS1	RS2	VS1	VS3
Preindustrial era (1800-1871)				
C-to-N	~12	>15	10-11	11-12
SCD			<1	
Zn	260	260	260	260
Midge community	Pro-Cry	Mic-Mon	Mic-Mon	Mic-Mon
First stage of industrialisation (1871-1925)				
C-to-N	12-14	15-17	9-10	10-12
SCD			1-2	
Zn	260	260	260	260
Midge community	Pro-Cry	Mic-Mon	Mic-Mon	Mic-Mon
		(*Chironomus* increasing)		
First period of rapid industrial growth (1925-1940)				
C-to-N	~14	12-15	~9	~11
SCD			2-4	
Zn	260-1000	260-500	260	260
Midge community	Chi-Pro	Chi ant	Chi ant	Chi ant
Building up modern industrial society (1940-1975)				
C-to-N	14-18	10-13	~9	9-11
SCD			4-21	
Zn	1000-22 000	500-3000	260-1100	260-760
Midge community	Chi plu→ desolate bottom	Chi plu	Chi ant	Chi ant

I. Preindustrial era (1800-1871)

Only 2 % of the human population in the province of Häme, to which the study area belongs, were living in towns in 1840 (Kaukovalta 1931). The number of inhabitants in Hämeenlinna, the only town in the area, in 1870 was 3100. Most of the population earned their living by farming. Agricultural productivity was low due to poor tillage methods and a scarcity of fertilizers. "Slash-and-burn" agriculture was therefore in general use during the 19th Century (Kaukovalta 1931). The low-lying fields and meadows near the shore of Vanajavesi were often flooded. Artificial water level lowering in Vanajavesi was carried out in order to obtain additional arable land. The last lowering, that of 1857, was no doubt the most significant human action to affect Lake Vanajavesi during the preindustrial era. Fishing was an important subsidiary occupation for the population. Economically the most important fish species were pike-perch (*Lucioperca lucioperca*) and bream (*Abramis brama*) (Hirviranta 1948).

The profundal zone of Vanajanselkä and Rauttunselkä was inhabited by a *Micropsectra - Monodiamesa* community similar to that of moderately oligotrophic lakes with a labile thermal stratification. The trophic level was appreciably lower than in the 20th Century. The oxygen content of the hypolimnion was high enough for polyoxybiontic midge species typical of the *Tanytarsus lugens* community to exist. High allocthonous humus inputs had lowered the productivity of the lake (a high C-to-N ratio in the sediments). It is probable that the artificial water level lowering in the 18th Century and in 1857 adversely affected the benthic community by reducing the availability of food materials.

II. The first stage of industrialization (1871-1925)

The establishment of a wood-pulp mill and paper factory at Valkeakoski in 1871 can be defined as the start of the industrial era in the history of the Vanajavesi region. New technology was coming rapidly into use for exploiting rich timber resources: a sulphate pulp mill in 1880 and a sulphite pulp mill in 1907 (Autio & Nordberg 1972). Valkeakoski arose in the form of an industrial centre. The production of its wood-processing industry increased during this period from a few hundred tons to 31 000 tons per year. The number of inhabitants in Valkeakoski increased from a few hundred to 3600. Kansanen & Aho (1981) estimated the total waste water load of Valkeakoski to correspond to a BOD load from the sewage of about 100 000 persons in 1924. The migration of the rural population into towns started at about this time. About 17 % of the population of the province of Häme were living in towns in 1920 (Typpö 1959). The municipal sewer network in use in most towns greatly increased the pressure on adjacent watercourses. This took place in Hämeenlinna in 1911, when the total number of inhabitants was 6400.

The first signs of increasing human impact were apparent from the character of Kärjenniemenselkä, just below Valkeakoski. Slight increases in the copper, dehydroabietic acid and C-to-N ratios indicate the beginnings of industrial impact on sediments. Oxygen conditions were, however, adequate for supporting a diverse midge fauna in which *Procladius* spp. and *Cryptotendipes* were characteristic species. The abundance of the midge fauna was low, indicating lower productivity than at a later time.

The profundal zone of Rauttunselkä and Vanajanselkä was colonised by a *Micropsectra - Monodiamesa* community, but the abundance of *Chironomus anthracinus*-gr. began to increase at the end of this period. The first signs of temporary oxygen depletion were seen in Vanajanselkä. The productivity of the lake began to increase. This is indicated by a slight increase in the sedimentary chlorophyll content and a decrease in the C-to-N ratio (cf. Table 11). By the 1920s the watercourse was already polluted in the Hämeenlinna region, and these waters undoubtedly affected the productivity of Vanajanselkä (Järnefelt 1929). The impact of the waste waters of Valkeakoski was probably restricted at this time to Kärjenniemenselkä and Rauttunselkä.

III. First period of rapid industrial growth (1925-1940)

Characteristic of the economic development between the two world wars was a rapid industrial growth based on wood-processing. Pulp and paper production increased in Valkeakoski from 31 000 to 78 000 tons (in 1937). This boom period ended with the advent of the second world war. Urbanisation continued. In Valkeakoski the number of inhabitants increased to 4700 and in Hämeenlinna it grew to 10 000.

The impact of rapidly increasing waste water loading was clearly apparent in Kärjenniemenselkä, where regular periods of oxygen depletion began to occur. The direct impact of the increased load from the wood-processing industry is indicated by a rise in the dehydroabietic acid content of the sediment. The productivity increased and the abundance of the total midge fauna and that of *Chironomus plumosus*-gr. increased rapidly. The oxygen conditions were, however, still good enough to support a diverse fauna in which *Procladius* spp. were among the dominant types.

The profundal zone of Rauttunselkä and Vanajanselkä began to suffer from the periodical oxygen depletion. The polyoxybiontic members of the *Micropsectra - Monodiamesa* community vanished from the profundal. The latter was subsequently colonised by the *Chironomus anthracinus* community. The diversity of the profundal fauna decreased. The trophic status of the lake increased, which is also indicated by the increase of the sedimentary chlorophyll content (Table 11). The zinc content in Vanajanselkä was still at its natural background level. The deterioration of water quality in Rauttunselkä resulted, for the first time, in fish deaths, although on a small scale over several summers during the 1930s (Selin 1982).

IV. Building up the modern industrial society (1940-1975)

Soon after World War II a rapid economic growth began, such as had never been seen before. The production of the wood-processing industry of Valkeakoski increased from 38 000 tons in 1945 to 342 000 tons in 1971. The industry became much more versatile. New industrial plants were founded, e.g. plywood, skin, pelt, potato flour, glue, glass, canning and sugar factories, dairies, abattoirs and a metal industry developed in the Valkeakoski and Hämeenlinna area. The most important of these was a chemical rayon fibre factory, which started production in 1943. Its fibre output increased up to 37 000 tons in 1972. The number of inhabitants increased in Valkeakoski from 4700 to 22 000 and in Hämeenlinna from 10 000 to 41 000. More than half of the population of the province of Häme was living in towns in the 1960s. The pressure on the watercourse increased rapidly. Ryhänen (1962) estimated that the BOD load from Valkeakoski was equivalent to that of 480 000 persons in 1954. Jokinen et al. (1974) estimated this figure in 1974 to be about 1 200 000. The corresponding figure for the Hämeenlinna region in 1954 was 266 000 (Ryhänen 1962). The importance of diffuse loading from agriculture, peatland ditchings, forestry and rural settlements also increased when new technology came into use. A new phenomenon was the building of summer cottages on the shores of lakes. Their total number in Vanajanselkä in 1969 was about 570 (Uotila 1971). Most of the waste waters were discharged into the lake without any purification taking place.

The strongly increased waste water loading from the wood-processing industry in the 1950s led to the complete and continuous anoxia in the deepwater region of Kärjenniemenselkä. Before the collapse of the deepwater midge fauna in 1957, the diversity decreased as the abundance of *Chironomus plumosus* increased and *Procladius* spp. vanished. The formation of annually laminated sediments commenced as the bottom fauna was destroyed. The zinc content of the sediment started to rise in the 1940s due to the waste waters of the rayon fibre factory. The littoral elements in the subfossil fauna after 1957 showed that oxygen conditions were still favourable to bottom animals in the shallow-water area.

In the profundal of Rauttunselkä the deterioration of the oxygen conditions lead to the development of a *Chironomus plumosus* community in the 1940s. The zinc content rose from its natural background level of 260 ppm to over 3000 ppm, indicating the impact of the waste waters of the Valkeakoski industries. These waste waters began to flow during the winter in the form of a density flow as far as Vanajanselkä, upstream along the watercourse. This is indicated by the rise in zinc content in the whole area of Vanajanselkä. The impact of the density flow was mainly restricted to the southwestern part of Vanajanselkä. The diversity of the *Chironomus anthracinus* community decreased even further. Productivity rose rapidly. This is reflected by a very strong increase in the sedimentary chlorophyll content. The deterioration of the oxygen conditions in late winter led to massive fish kills in the spring of 1972 and 1974, when thousands of kilograms of fish died as a result of the upwelling of anaerobic waste liquour after the breaking up of the ice cover (Jokinen et al. 1972, 1974).

V. Start of industrial and municipal pollution control (1975-)

The strong deterioration in the general state of all sub-basins of Vanajanselkä led to the first significant pollution control actions both in industry and in the towns of the area. In the wood-processing industry the most important actions were the introduction of a washing plant and a chemicals recovery plant at the sulphite pulp mill in Valkeakoski (1975). Liming of the acid waste waters and recovery of zinc was begun at the rayon fibre factory in 1980. Municipal central sewage treatment plants for the towns also came into use and their efficacy in nutrient reduction was a great improvement. Thanks to these purification plants, the total waste water load discharged into Vanajavesi stopped increasing after 1975. The density flow of the industrial waste waters of Valkeakoski was also prevented by means of aerators sited in the narrow sound between Rauttunselkä and Vanajanselkä.

The slight improvement in the state of Kärjenniemenselkä reported by the water authority and by Kansanen & Aho (1981) is reflected by an increase in the influx of littoral chironomids after 1975. The water depths, however, were still barren. In Rauttunselkä and Vanajanselkä no improvement could be seen from the profiles. This is due to bioturbation, which reduces the time resolution of these profiles.

5. Concluding remarks

The redeposition of midge remains originating from shallow-water erosion bottoms or transportation bottoms, which may occur even in the deepwater area (Kansanen & Jaakkola 1985), in many lakes is the most significant factor tending to obscure palaeolimnological interpretation of the subfossil thanatocoenoses in the deepwater cores. Redeposition may significantly alter the species composition and highly add to the midge remain influx. In these cases misinterpretations can be avoided if identifications are made as far as possible and the results are compared with the live fauna at various depth zones. It is also necessary to compare thanatocoenoses from several cores.

Another difficulty is the fact that due to bioturbation the time resolution is reduced in those profiles where an abundant midge fauna is present (cf. Kansanen & Jaakkola 1985). In the case of annually laminated sediments, the time resolution is excellent, but there is no sedentary bottom fauna. A diverse midge thanatocoenose may be found in these cores, but it indicates conditions in the shallow-water zone.

In spite of these difficulties, midge analysis constitutes a useful palaeolimnological technique. A high number of species having different environmental requirements offers an abundance of information respecting past conditions in the lake, and not only from the typological point of view, as the midge analysis also offers hints concerning the water level changes in the basin.

In Lake Vanajavesi eutrophication led to the replacement of an oligotrophic *Micropsectra - Monodiamesa* community by a eutrophic Chironomus anthracinus community in the first decades of this century. The replacement took place at a relatively low loading level; about 1/10–1/5 of the present total waste water load. This is in accord with the established fact that Vanajavesi, like many other lakes in the clay area of southern Finland, was originally eutrophic. The dysoligotrophic features are due to a high humus load. Artificial lowering of the water levels also probably adversely affected the food availability for the midge fauna. A relatively slight cultural impact was needed to cause a return of the eutrophic conditions.

In the further succession from a *Chironomus anthracinus* community to a *Chironomus plumosus* community, and finally to the disappearance of the deepwater fauna, the key factor appears to have been the oxygen content of the water. The oxygen state of Lake Vanajavesi depends not only on the production level of the lake, but more on the direct impact of waste water loading having a high BOD. The main goal in future water protection work should be the curtailing of areas suffering from severe oxygen depletion. Because a water ecosystem having a *Chironomus anthracinus* type of community in the profundal zone is also highly productive from the fishery standpoint, realistic goals underlying protection efforts on behalf of Lake Vanajavesi could be the returning of this community to the profundal of Rauttunselkä and the preservation of the community in Vanajanselkä. In Kärjenniemenselkä the colonisation of the deepwater area by a stable *Chironomus plumosus* community would be possible in this case. This situation would correspond to that prevalent in Lake Vanajavesi probably in the early 1940s.

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