

RESPONSES OF THE MACROZOOBENTHOS TO WATER-BLOOMS IN THE EUTROPHIED BROWN-WATER LAKE VALGUTA MUSTJÄRV, SOUTH ESTONIA

Tarmo TIMM, Külli KANGUR, Henn TIMM, and Viivi TIMM

Võrtsjärv Limnological Station, Institute of Zoology and Botany, Estonian Academy of Sciences, EE-2454 Rannu, Tartumaa, Estonia

Presented by K. Elberg

Received October 1, 1993; accepted October 13, 1993

Abstract. In 1978–1983 mineral fertilizers were applied in the watershed and the lake was enriched with nutrients. Two waves of water-blooms, dominated by different algal communities, were observed. Different groups of bottom invertebrates responded to water-blooms with waves of increased abundance after a different time. *Chironomus plumosus* determined the abundance and biomass of zoobenthos in the central part of the lake. From 1990 on, the previous moderate level of the zoobenthos has been restored despite continuing water-blooms.

Key words: macrozoobenthos, water-bloom, eutrophied lake.

INTRODUCTION

The anthropogenic eutrophication of Estonian lakes has been studied both in light-water lake types (Timm, 1991) and in brown-water (dystrophic and dyseutrophic) lakes (Timm et al., 1993). A tendency toward a gradual increase in the zoobenthos biomass during several decades was observed in both cases. The paper on brown-water lakes did not include the shallow brown-water Lake Valguta Mustjärv. However, this lake deserves special treatment as continuous observations have been carried out on it for 15 years, including periods of rapid eutrophication and partial recovery.

DESCRIPTION OF THE LAKE

Lake Valguta Mustjärv is situated in the county of Tartu, South Estonia, 1.7 km from the eastern shore of the large Lake Võrtsjärv and 2 km from the Võrtsjärv Limnological Station, 42.1 m above sea level. It has a surface area of 23.3 ha and maximum depth of about 1 m (Mäemets, 1968). The lake is surrounded by peat-bogs covered with pine forests. The southernmost and biggest of the several ditches flowing into the lake drains a recently (1986) abandoned industrial peat-field that produced peat dust. A canal flowing out of Lake Valguta Mustjärv to Lake Võrtsjärv via the Nigula Stream carries up to 50–55 l·sec⁻¹ of water in spring time but can dry up during drought. The annual turnover rate of the lake water is at least 1. It belongs to shallow soft-water dyseutrophic

lakes, subtype DE² according to Mäemets (1974), with total alkalinity of about 30 mg·l⁻¹, greatly variable dichromate oxidizability (24—117 mg O·l⁻¹ observed), pH mostly 6—6.6, and yellowish-brown to dark brown water colour. Most of the bottom is covered with liquid dark brown dy, except on some bare peat grounds near the eastern and northern shores. The western and the southern shores represent a quagmire bordered by a zone of *Nymphaea* spp., *Nuphar lutea*, and *Potamogeton natans* (Fig. 1). Scattered flecks of *Nuphar pumila* and *Potamogeton praelongus* occur in the central part. The whole water layer warms up to over +20°C on hot summer days, without any permanent stratification. Fish-kills occur in some winters.

MATERIAL AND METHODS

Samples of zoobenthos (9—12 times a year) were collected from January 1979 till July 1993 on one station in the middle of the lake. In summer 1986 they were taken every week. Four additional sampling sites in different parts (Fig. 1) were studied seasonally (January—February, May, July, and October) in 1979—1982, and only in July in 1983—1988 and 1991—1993. Altogether 275 samples were used, including 175 samples from the central part and 25 samples from every other station.

Every sample consisted of three hauls with the Borutski bottom grab (a modification of the Ekman grab, with 15 × 15 cm sampling area, 40 cm high). The sediment was washed on a silk sieve with 0.4—0.6 mm mesh size (14 threads per cm), macroscopic animals were picked out alive, preserved in ethanol, and weighed on torsion scales.

Data on water chemistry and the phytoplankton were obtained from the unpublished observation files of the Vörtsjärv Limnological Station.

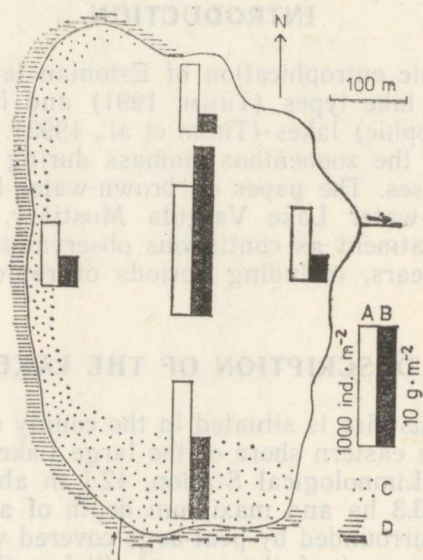


Fig. 1. Lake Valguta Mustjärv. Location of five sampling sites, average abundance and biomass of macrozoobenthos on them (without *Anodonta*) in July, 1979—1993. A — abundance, B — biomass (wet weight), C — continuous zone of floating-leaved macrophytes, D — riparian quagmire.

QUALITATIVE COMPOSITION OF THE BOTTOM FAUNA

Chironomidae larvae were the dominant group in every respect (over a half of the abundance, biomass, and number of species). Fifty taxa of them were found (those marked with an asterisk were identified after the imago): *Ablabesmyia longistyla* Fittkau, *A. phatta* (Egger), **Procladius choreus* (Meigen), *P. ferrugineus* (Kieffer), *P. nigriventris* Kieffer, **P. signatus* (Zett.), *Tanypus kraatzi* (Kieffer), *T. vilipennis* (Kieffer), *Cricotopus sylvestris* (Fabr.), *C. flavocinctus* (Kieffer), *Psectrocladius dilatoris* Zel., *P. zetterstedti* Brundin, *P. simulans* (Joh.), *Camptochironomus tentans* Fabr., *Chironomus cingulatus* Meigen, **C. plumosus* (L.), *C. solitus* Lin. et Erb., *Cladopelma viridula* (L.), *Cryptochironomus defecatus* (Kieffer), **Demicryptochironomus vulneratus* (Zett.), *Dicrotendipes lobiger* (Kieffer), *D. nervosus* (Staeger), **D. pulsus* (Walker), *Einfeldia carbonaria* (Meigen), *Endochironomus albipennis* (Meigen), *E. impar* (Walker), *E. tendens* (Fabr.), **Glyptotendipes glaucus* (Meigen), *G. gripekoveni* (Kieffer), *G. paripes* (Edw.), *Microchironomus tener* (Kieffer), *Microtendipes pedellus* (De Geer), *Pagastiella orophila* (Edw.), *Parachironomus arcuatus* (Goetgh.), **Pentapedilum sordens* (v. d. Wulp), *Phaenopsectra* sp., *Polypedilum bicrenatum* Kieffer, *P. gr. convictum* (Walker), *P. tetracrenatum* Hirv., *Stictochironomus rosenschoeldi* (Zett.), **Cladotanytarsus atridorsum* Kieffer, *C. gr. mancus* (Walker), **C. vanderwulpi* (Edw.), *Stempellina minor* (Edw.), *Tanytarsus excavatus* Edw. (or *T. nemorosus* Edw.), **T. gregarius* Kieffer, *T. holochlorus* Edw. (or *T. occultus* Brundin or *T. volgensis* Miseiko), *T. gr. lugens* Kieffer, *T. medius* Reiss et Fittkau, *T. verralli* Goetgh. Among them, *Chironomus plumosus* formed an absolute majority in the periods of mass occurrence but disappeared in some other periods. A few data on the chironomids of this lake were published by Kangryp (Kangryp, 1990).

Other dipterans were represented by the larvae of *Chaoborus flavicans* (Meigen) and various Ceratopogonidae, including large *Sphaeromias fasciatus* (Meigen). Among other insects, large larvae of *Sialis sordida* Klst. were the most common. The dragonflies *Cordulia aenea* L. (? or *C. aenoturfosa* Forster), *Libellula quadrimaculata* L., *Erythromma najas* (Hans.), and *Epitheca bimaculata* (Charp.); the mayfly *Caenis horaria* (L.); and the caddisflies *Agrypnia pagetana* Curt., *Cyrnus flavidus* McL., and *Oecetis furva* (Ramb.) occurred rarely and as single larval individuals. Some *Asellus aquaticus* L. and undetermined Hydracarina represented other arthropods.

A flourishing population of the large mussel *Anodonta stagnalis* (Gmelin) inhabited the central part of the lake, with an average abundance of 1.7 ind.·m⁻² and biomass 278 g·m⁻². The biggest specimen was about 15 years old and weighed 540 g when alive (420 g without mantle cavity water, 110 g the bare shell). They were not taken into consideration when calculating the abundance and biomass of the whole zoobenthos. Smaller molluscs were represented mostly by Pisidiidae: *Euglesa ruut* Timm and *E. fragilis* (Clessin), less often also *E. turgida* (Clessin), *E. milium* (Held), and *Amesoda scaldiana* (Normand). Only a single gastropod *Anisus albus* (Müller) was found.

The oligochaetes *Limnodrilus hoffmeisteri* Clap. and *Potamothrix hammoniensis* (Mich.) were rather common while *Dero obtusa* Udekem, *D. digitata* (Müller), *Nais pardalis* Piguët, and *Specaria josinae* (Vejd.) were rare. The leeches *Erpobdella octoculata* (L.), *Helobdella stagnalis* (L.), *Hemiclepsis marginata* (Müller), and *Glossiphonia complanata* (L.) occurred also seldom.

ABUNDANCE AND BIOMASS

The average abundance of bottom macroinvertebrates in the whole lake during 1979—1982 was $929 \pm 132 \text{ ind.} \cdot \text{m}^{-2}$, the biomass was $6.2 \pm 1.9 \text{ g} \cdot \text{m}^{-2}$ ($p \leq 0.05$, wet weight). There occurred no summer minimum of the zoobenthos, connected with the simultaneous emergence of water insects. Moreover, the summer biomass appeared the highest, due to the great abundance of large *Chironomus plumosus* larvae. The species is probably multivoltine in this well-warming lake. Its total abundance was the highest in autumn (Fig. 2). During the whole observation period the average summer (July) numbers of the zoobenthos fluctuated greatly in different years, with 412—1500 $\text{ind.} \cdot \text{m}^{-2}$ of abundance and 1.3—14.6 $\text{g} \cdot \text{m}^{-2}$ of biomass. However, the summer mean values of many years were rather close to the above all-year abundance and biomass: $868 \pm 222 \text{ ind.} \cdot \text{m}^{-2}$ and $5.7 \pm 2.2 \text{ g} \cdot \text{m}^{-2}$. Against the background of Estonian lakes in general (Mäemets, 1968), this corresponds to a low level of abundance but to a moderate or even high level of biomass.

Two sampling sites appeared to be the richest: the southern end among the thickets of *Nuphar* and *Nymphaea* (functioning like a biofilter for the main inflow), and the middle of the lake where planktonogenous detritus was deposited (Fig. 1).

Underestimations may occur as a result of the deep vertical distribution of animals inside the sediment. On March 29, 1988, the mid-lake sample was divided into 7 layers (0—10, 10—15, 15—20, 20—25, 25—30, 30—35, and 35—40 cm). Chironomidae and Ceratopogonidae were met in all the layers. Probably a small number of them can be distributed even deeper in the mud and so escape the grab. Oligochaeta occurred at the depths of 0—20 cm, and Pisidiidae only in the uppermost layer.

CHANGES IN THE WATER ENVIRONMENT

In the 1950s the lake was relatively clean, with well-transparent brown water, pH 7.5 (July 1953 and June 1956) and dichromate oxidizability 48.9 $\text{mg O} \cdot \text{l}^{-1}$ (July 1953). The phytoplankton was poor in species and not very abundant in July 1962, the dominating species was *Microcystis aeruginosa* Kütz., which caused also a water-bloom (Mäemets, 1968). No water-bloom occurred in 1967 (Raia, 1972). Water-mosses (*Fontinalis*) were abundant in different parts of the lake.

Intensive research on the lake was started by the Võrtsjärv Limnological Station only in 1979 when the danger of a rapid eutrophication became apparent. In 1978—1983 turf for creating green areas in towns was cultivated on the exhausted peat fields south of the lake. In 1978, 20.755 metric tons of different mineral fertilizers (among them 16.65 tons of oil-shale ash) was applied on 3.11 ha of experimental grass fields. In all probability, the amount was much greater during the following years of commercial cultivation. Part of the fertilizers was carried into the lake with drainage water. Turf-raising on the watershed was stopped in 1983.

The water became more acid, with pH 5.4—7.0 (7.3 only once, in 1987) while dichromate oxidizability varied in broad limits. The winter concentration of oxygen decreased down to 7—20% in March 1979—1982. Up to 200—1000 $\text{mg} \cdot \text{m}^{-3} \text{NO}_3^-$ was found in the water in some autumn and winter months of 1979—1981.

Total P and N were measured monthly in 1984—1987, and twice in 1992 and 1993. Their concentrations fluctuated irregularly in different months, mostly within the limits corresponding to the hypertrophic state (*sensu* Milius et al., 1991). The N/P ratio was also very variable but annual trends of both biogenic elements were parallel. The decrease in total P during 1984—1987 was related to the cessation of fertilizing the

watershed in 1984 as well as to the general tendency of Estonian small lakes, caused by climatic factors in the 1980s (Milius et al., 1991). In 1992—1993 the concentration of total P in the lake water apparently stabilized near the level of 1987. Probably, the phosphorus accumulated in the sediment continued its circulation in the lake.

The phytoplankton still revealed a relatively low biomass in the summer of 1979, about $4 \text{ g} \cdot \text{m}^{-3}$, with the predominance of the cyanobacterium *Microcystis aeruginosa*. During the following period up to 1983 ever-growing phytoplankton blooms were observed every summer, with a biomass of about $20 \text{ g} \cdot \text{m}^{-3}$ and chlorophyll *a* concentration $30\text{--}60 \text{ mg} \cdot \text{m}^{-3}$ in 1982—1983 (Fig. 3). Different algae dominated in the phytoplankton, with the small green alga *Tetraëdron minimum* (A. Br.) Hansg. being the most constant. In 1980—1981 even a winter water-bloom of the chrysophyte alga *Synura* sp. was observed under the ice.

In 1984, immediately after the stopping of the heavy external loading, no water-bloom was observed. The algal biomass did not exceed $4.5 \text{ g} \cdot \text{m}^{-3}$ that year (Fig. 3). From 1985 on, a new period of water-blooms began, apparently caused by the intralacustrine turnover of biogenic elements. The annual trends of the concentrations of the phytoplankton and total P in the water, when available, coincided (Figs. 3 and 4). The biomass of the phytoplankton reached $70 \text{ g} \cdot \text{m}^{-3}$ (with $373 \text{ mg} \cdot \text{m}^{-3}$ chlorophyll *a*) in July 1988. In several summers the lake surface was often covered with a bluish foam while the water itself appeared grey and turbid. New dominants occurred in the phytoplankton of this period: cyanobacteria *Anabaena* spp. at the peak of every water-bloom, the euglenophyte alga *Gonyostomum semen* (Ehrg.) Dies. before and after it. As a result of the abundant production of algal detritus, a thin layer of black mud accumulated on the surface of brown dy in the central part of the lake. No water-blooms were observed in 1993.

CHANGES IN THE AMOUNT OF ZOOBENTHOS IN GENERAL

In July 1953, the zoobenthos of the lake was scanty, $417 \text{ ind.} \cdot \text{m}^{-2}$ and $7.2 \text{ g} \cdot \text{m}^{-2}$ on an average, with Ephemeroptera and Odonata as dominating groups. The Chironomidae formed an insignificant minority (Mäemets, 1968). In the same month of 1979, after several decades of commercial peat production on the watershed, the average abundance and biomass of the zoobenthos remained almost the same but with considerable variations in different parts of the lake ($412 \pm 163 \text{ ind.} \cdot \text{m}^{-2}$ and $5.6 \pm 5.2 \text{ g} \cdot \text{m}^{-2}$). The Chironomidae had risen to the first place, especially in the middle of the lake where *Chironomus plumosus* was already abundant. On the central station, the average abundance of the zoobenthos measured $815 \pm 466 \text{ ind.} \cdot \text{m}^{-2}$, the biomass $20.9 \pm 18.7 \text{ g} \cdot \text{m}^{-2}$ while the respective average numbers for all other stations were only $311 \pm 119 \text{ ind.} \cdot \text{m}^{-2}$ and $1.8 \pm 1.2 \text{ g} \cdot \text{m}^{-2}$. *Chaoborus flavicans* occurred in different parts of the lake, and so did Oligochaeta, Pisidiidae, Ceratopogonidae, Odonata, *Sialis*, *Asellus*, and Hirudinea.

During a few following years when fertilizers were applied on the watershed, the average summer abundance of the zoobenthos increased roughly threefold, up to $1433 \pm 584 \text{ ind.} \cdot \text{m}^{-2}$ (in 1984), the biomass up to $14.6 \pm 7.6 \text{ g} \cdot \text{m}^{-2}$ (in 1982). This happened mostly due to an explosive multiplication of *Chironomus plumosus* in the central part of the lake. A gradual decrease followed, down to $418 \pm 98 \text{ ind.} \cdot \text{m}^{-2}$ and $1.3 \pm 0.6 \text{ g} \cdot \text{m}^{-2}$ in July 1991, in spite of repeated water-blooms. In July 1993, after the cessation of water-blooms, the record average abundance of $1500 \pm 760 \text{ ind.} \cdot \text{m}^{-2}$ was observed mostly on the account of smaller Chironomidae while the biomass of zoobenthos remained moderate, $5.2 \pm 3.4 \text{ g} \cdot \text{m}^{-2}$.

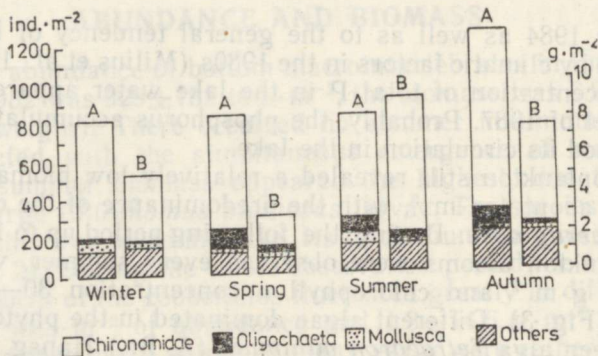


Fig. 2. Average abundance (A) and biomass (B, wet weight) of macrozoobenthos (without *Anodonta*) in Lake Valguta Mustjärv in different seasons of 1979—1982.

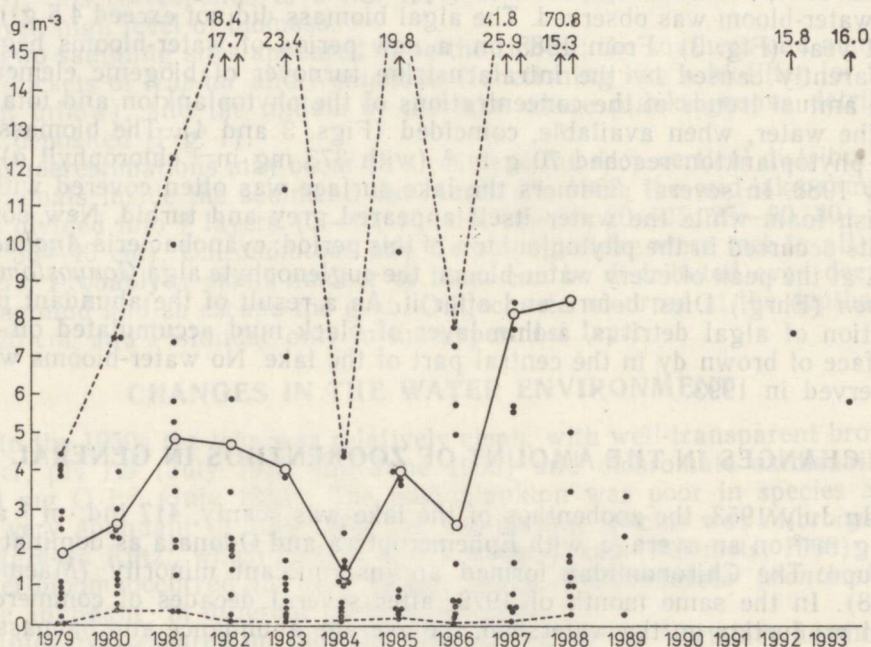


Fig. 3. Fluctuations of the biomass of phytoplankton (wet weight) in Lake Valguta Mustjärv, 1979—1993. Dots correspond to monthly measurements, dashed lines to their yearly upper and lower limits observed. Circles and solid lines show the annual arithmetic means and their changes.

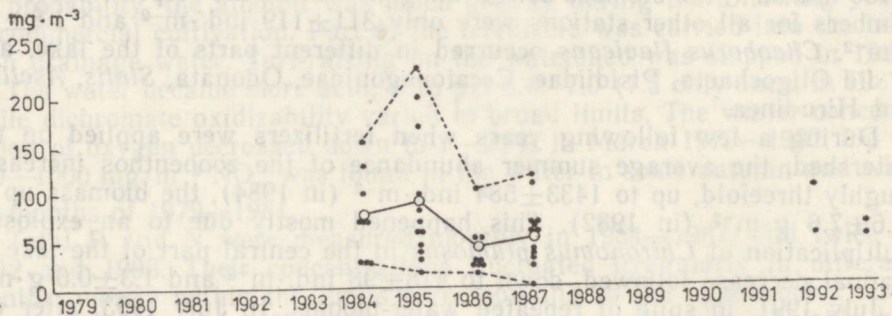


Fig. 4. Fluctuations of the concentration of total phosphorus in the water of the central part of Lake Valguta Mustjärv. Graphs as in Fig. 3.

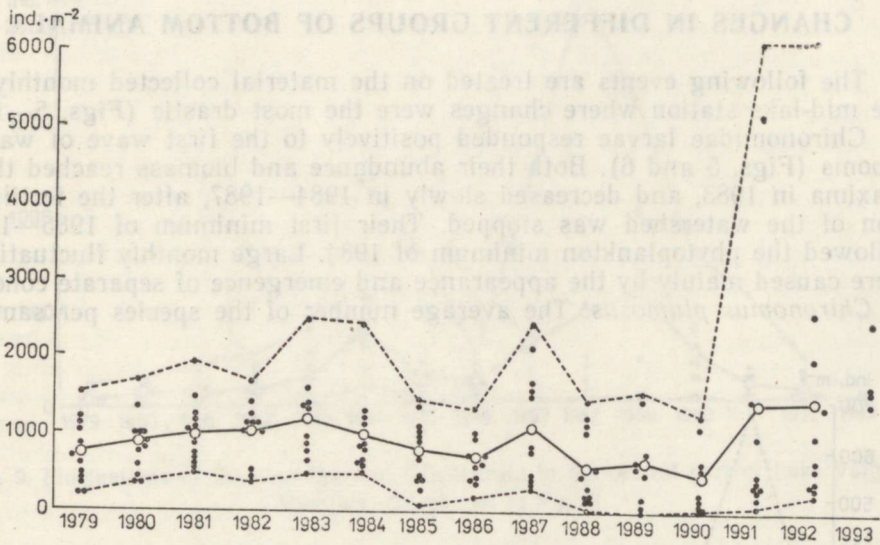


Fig. 5. Fluctuations of the abundance of Chironomidae larvae in the central part of Lake Valguta Mustjärv. Graphs as in Fig. 3.

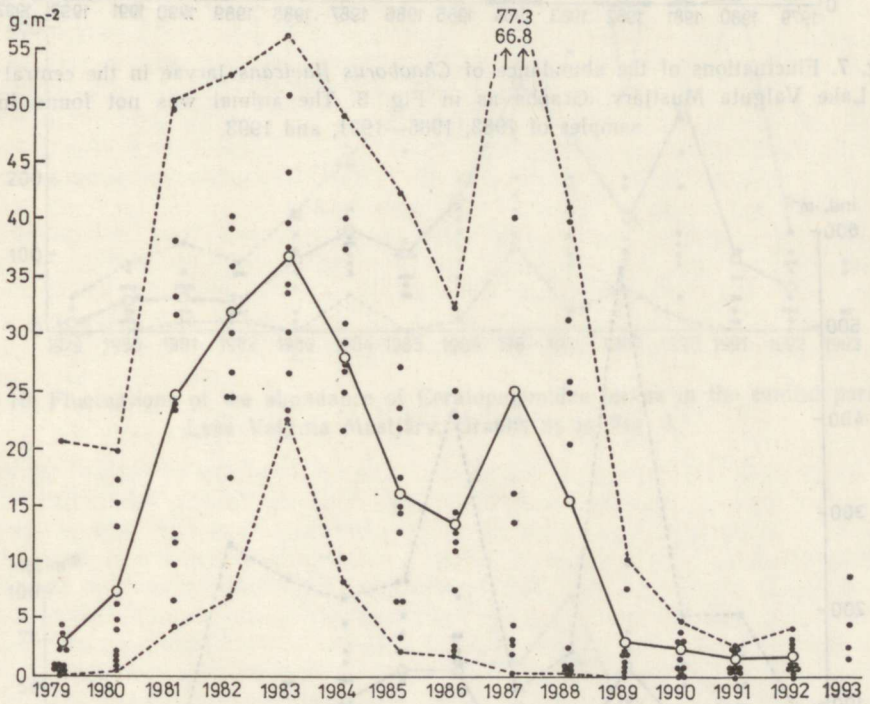


Fig. 6. Fluctuations of the biomass of Chironomidae larvae (wet weight) in the central part of Lake Valguta Mustjärv. Graphs as in Fig. 3.

CHANGES IN DIFFERENT GROUPS OF BOTTOM ANIMALS

The following events are treated on the material collected monthly at the mid-lake station where changes were the most drastic (Figs. 5—11).

Chironomidae larvae responded positively to the first wave of water-blooms (Figs. 5 and 6). Both their abundance and biomass reached their maxima in 1983, and decreased slowly in 1984—1987, after the fertilization of the watershed was stopped. Their first minimum of 1985—1986 followed the phytoplankton minimum of 1984. Large monthly fluctuations were caused mainly by the appearance and emergence of separate cohorts of *Chironomus plumosus*. The average number of the species per sample

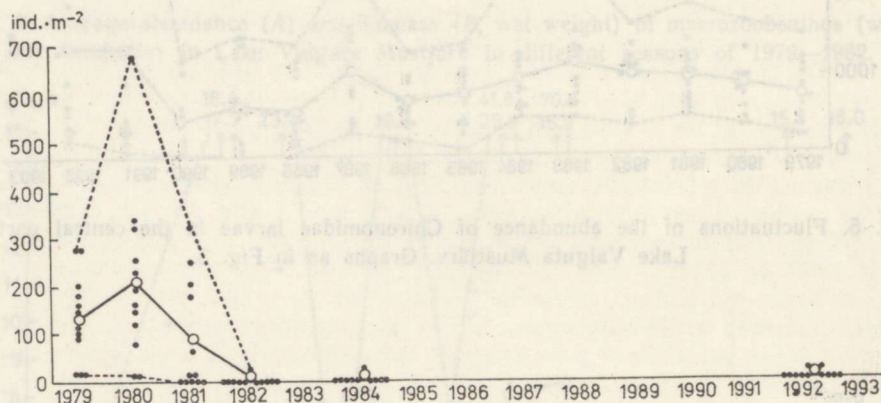


Fig. 7. Fluctuations of the abundance of *Chaoborus flavicans* larvae in the central part of Lake Valguta Mustjärv. Graphs as in Fig. 3. The animal was not found in the samples of 1983, 1985—1991, and 1993.

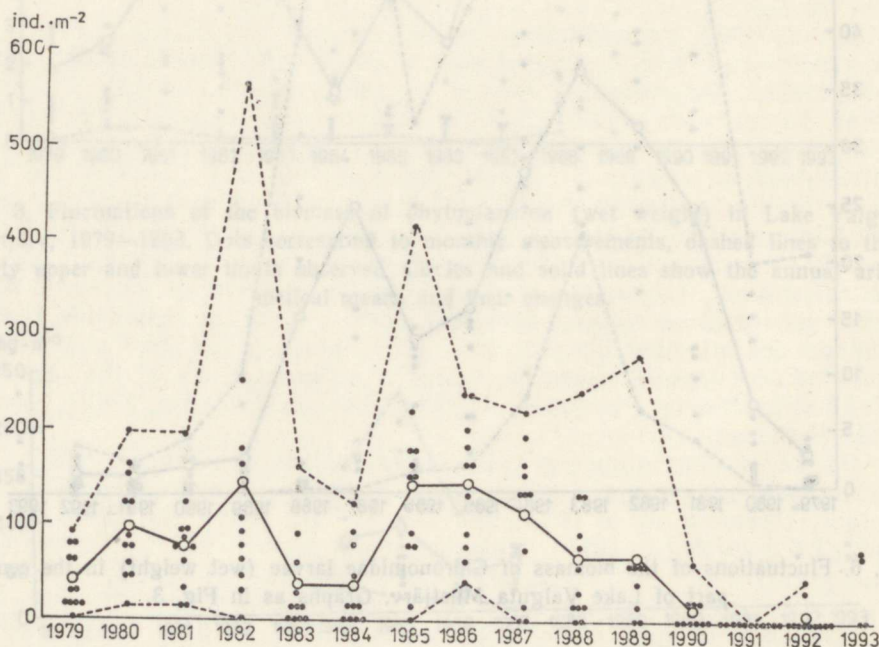


Fig. 8. Fluctuations of the abundance of Pisiidiidae in the central part of Lake Valguta Mustjärv. Graphs as in Fig. 3.

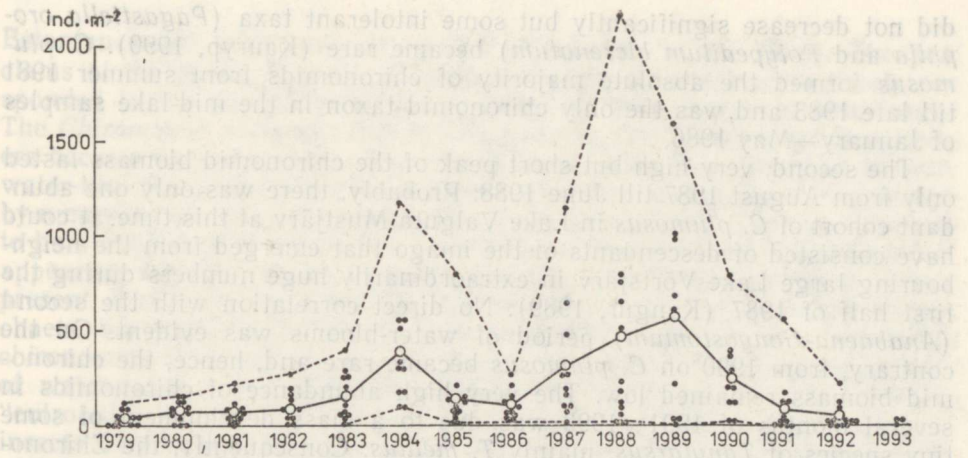


Fig. 9. Fluctuations of the abundance of *Oligochaeta* in the central part of Lake Valguta Mustjärv. Graphs as in Fig. 3.

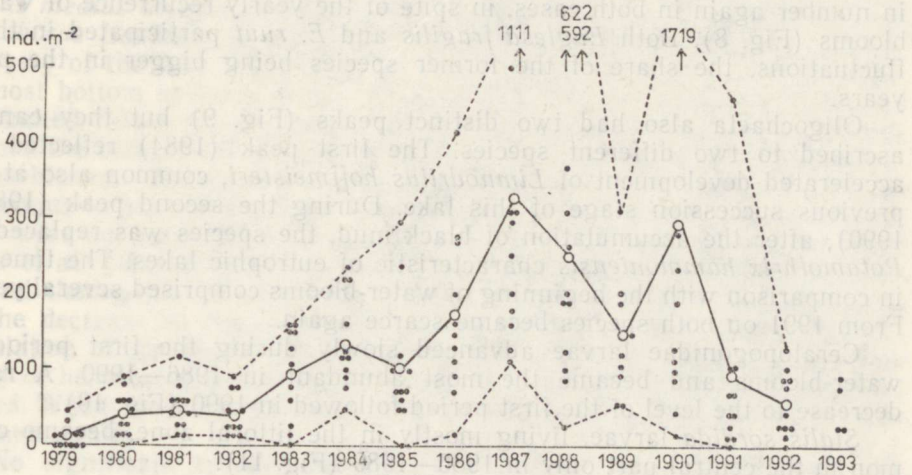


Fig. 10. Fluctuations of the abundance of *Ceratopogonidae* larvae in the central part of Lake Valguta Mustjärv. Graphs as in Fig. 3.

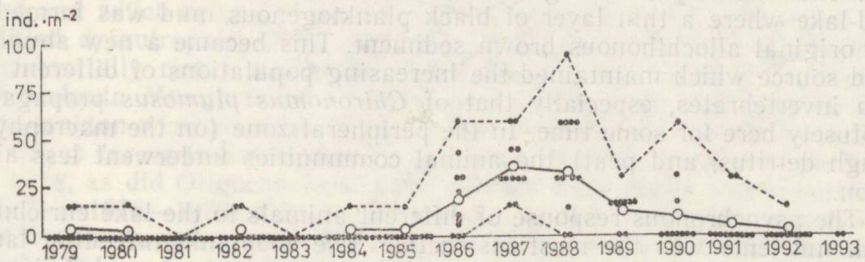


Fig. 11. Fluctuations of the abundance of *Sialis sordida* larvae in the central part of Lake Valguta Mustjärv. Graphs as in Fig. 3.

did not decrease significantly but some intolerant taxa (*Pagastiella orophila* and *Polypedilum bicornatum*) became rare (Kangur, 1990). *C. plumosus* formed the absolute majority of chironomids from summer 1981 till late 1983 and was the only chironomid taxon in the mid-lake samples of January—May 1986.

The second, very high but short peak of the chironomid biomass lasted only from August 1987 till June 1988. Probably, there was only one abundant cohort of *C. plumosus* in Lake Valguta Mustjärv at this time. It could have consisted of descendants of the imago that emerged from the neighbouring large Lake Vörtsjärv in extraordinarily huge numbers during the first half of 1987 (Kangur, 1989). No direct correlation with the second (*Anabaena-Gonyostomum*) period of water-blooms was evident. On the contrary, from 1990 on *C. plumosus* became rare and, hence, the chironomid biomass remained low. The very high abundance of chironomids in several months of 1991—1993 was due to a mass development of some tiny species of *Tanytarsus*, mainly *T. medius*. Consequently, the Chironomidae took a different attitude to the two separate waves of water-blooms.

The dipteran larvae *Chaoborus flavicans* appeared to be rather intolerant to rapid eutrophication. After a small peak in 1980 they became practically extinct already in the second half of 1981 (Fig. 7).

Pisidiidae became rather numerous at the beginning of both water-bloom periods. After 3—4 years of great abundance pea clams decreased in number again in both cases, in spite of the yearly recurrence of water-blooms (Fig. 8). Both *Euglesa fragilis* and *E. ruut* participated in these fluctuations, the share of the former species being bigger in the peak years.

Oligochaeta also had two distinct peaks (Fig. 9) but they can be ascribed to two different species. The first peak (1984) reflected the accelerated development of *Limnodrilus hoffmeisteri*, common also at the previous succession stage of this lake. During the second peak (1987—1990), after the accumulation of black mud, the species was replaced by *Potamothrix hammoniensis* characteristic of eutrophic lakes. The time-lag in comparison with the beginning of water-blooms comprised several years. From 1991 on both species became scarce again.

Ceratopogonidae larvae advanced slowly during the first period of water-blooms and became the most abundant in 1986—1990. A rapid decrease to the level of the first period followed in 1990 (Fig. 10).

Sialis sordida larvae, living mostly in the littoral zone, became common in the central part only in 1986—1989 (Fig. 11).

DISCUSSION

Lake Valguta Mustjärv provided a rare opportunity to follow different stages of rapid eutrophication of a small lake, including its partial recovery. The intensity of changes in the zoobenthos was the highest in the mid-lake where a thin layer of black planktogenous mud was formed on the original allochthonous brown sediment. This became a new abundant food source which maintained the increasing populations of different bottom invertebrates, especially that of *Chironomus plumosus* propagating profusely here for some time. In the peripheral zone (on the macrophytes, rough detritus, and peat) the animal communities underwent less alteration.

The asynchronous response of different animals to the lake enrichment with nutrients was the most instructive. The zooplankton-feeding larvae of *Chaoborus flavicans*, known as being very tolerant to oxygen deficiency, vanished after a short peak at the very beginning of enrichment. Their decrease in the case of eutrophication was observed earlier when different

Proc. Estonian Acad. Sci. Biol. 1991, 1: 3-11

Estonian small lakes were compared (Смирнова et al., 1980). The peacocks of the genus *Euglesa* as surface-feeding filtrators immediately responded to the additional detritus production with increased abundance. The *Chironomus plumosus* larvae as gathering and filtrating detritus-feeders became very abundant after two to three years from the start of both water-bloom periods. Their second peak was short and probably supported by numerous unusual immigrants from Lake Võrtsjärv. *C. plumosus* seemed to be a temporary inhabitant in Lake Valguta Mustjärv, appearing and disappearing together with the most favourable nutritional conditions. When present, it usually dominated in the central part of the lake. The Oligochaeta, burrowing deposit-feeders, reached their peaks one year later than chironomids. Different oligochaete species dominated after different periods of water-blooms: the ubiquitous *Limnodrilus hoffmeisteri* first, and the "eutrophic" *Potamothrix hammoniensis* later on. The mostly predatory insects Ceratopogonidae and *Sialis* (for their nutrition see Глухова, 1979, and Giani & Laville, 1973, respectively) reached their maxima last.

Finally, the abundance of all these animals was reduced to a level comparable with that of 1979, or even lower. The deposit-feeders and filtrators reached their minima in 1990 (seven years after the end of the lake enrichment), part of the predators (Ceratopogonidae) even later. During some seasons of 1991—1993 another, a very small chironomid larva *Tanytarsus medius* became abundant. The reappearance of a few individuals of *Chaoborus flavicans* in 1992 also deserves attention. Evidently, a slow recovery of the lake has begun. As water-blooms continued, the decrease of most bottom animals cannot be caused by detritus shortage. They can be limited rather by its quality, since different algae and cyanobacteria formed the bulk of the primary production during the different periods of water-blooms. The cyanobacteria *Anabaena* and their remains can be poisonous to some extent and therefore they are avoided by *C. plumosus*; they were not mentioned as occurring in the gut of this species by Izvekova et al. (Извекова et al., 1983). The living flagellates *Gonyostomum* defend themselves by excreting a large amount of slime. Another cause of the decrease in the abundance of the zoobenthos can lie in the self-regulation of the bottom animal community. After an explosive development of herbivores and detritus-feeders, a wave of predatory insects followed. When predators gained control over their prey, their abundance decreased again.

No significant correlations occurred between water-blooms and the changes of zoobenthos in Lake Valguta Mustjärv ($p \leq 0.1$). They do not coincide in time, although their causal relations are doubtless, at least during the first stages of eutrophication. An analogical 2—3-year lag in the response of zoobenthos to changes in the trophic state was noted by Giziński (1988) in the case of several Polish lakes.

Among the 10 Estonian lakes which were studied shortly in the same period and which belong to the same limnological subtype (soft-water unstratified dyseutrophic, DE²) only lakes Mäha, Rummu, and Käsmu had a substantially richer zoobenthos ($> 2000 \text{ ind.} \cdot \text{m}^{-2}$, $> 10 \text{ g} \cdot \text{m}^{-2}$) than Lake Valguta Mustjärv. In all these three lakes both macrophytes and phytoplankton were abundant. Besides the *Chironomus*, also Mollusca and *Gammarus lacustris* Sars formed a great deal of the biomass in the first two lakes, as did Oligochaeta in Lake Käsmu. Lake Mäha was repeatedly studied in 1976—1979; a 2—3-fold increase in the zoobenthos abundance and biomass was observed against the background of rapid eutrophication (Тимм, 1991, and unpublished data).

Several brown-water lakes belonging to other subtypes (soft-water stratified dyseutrophic, DE¹; and unstratified dystrophic, D³, according Mäemets, 1974) mostly exhibited a similar or lower quantitative level of zoo-

benthos as Lake Valguta Mustjärv. A tendency to a slow increase in the abundance and biomass manifested itself in several repeatedly studied lakes. However, one of them, Lake Neeruti Sinijärv (subtype DE¹) appeared extraordinarily zoobenthos-rich in 1988. An average biomass of $69.5 \pm \pm 32.3 \text{ g} \cdot \text{m}^{-2}$ was observed in the littoral, mainly due to the mass occurrence of *Chironomus* spp., but only $0.3 \pm 0.2 \text{ g} \cdot \text{m}^{-2}$ in the profundal (Timm et al., 1993, and unpublished data). The example of Lake Valguta Mustjärv suggests that in the cases of exceptionally copious zoobenthos, observed in a few brown-water lakes, the conditions are unstable due to rapid eutrophication. The temporary high abundance and biomass of bottom animals can decrease again when the community stabilizes.

ACKNOWLEDGEMENTS

The authors are greatly indebted to Dr. Reet Laugaste for data on phytoplankton and hydrochemical conditions, and to Mrs. Ester Jaigma for linguistic help.

REFERENCES

- Giani, N., Laville, H. 1973. Cycle biologique et production de *Sialis lutaria* L. (Megaloptera) dans le Lac de Port-Bielh (Pyrénées Centrales). — *Annls. limnol.*, 9, 1, 45—61.
- Giziński, A. 1988. Bottom fauna of 6 lakes in Brodnica Lake District and 10 lakes in Tuchola Forests. — *Acta Univ. N. Copernici, Toruń, Nauki Matem.-Przyrod.*, 65, *Prace Limnologiczne*, 16, 51—73.
- Kangur, K. 1989. Ecology and population dynamics of *Chironomus plumosus* L. in Lake Võrtsjärv, Estonian S.S.R. — *Acta Biol. Debr. Oecol. Hung.*, 3, 189—198.
- Milius, A., Saan, T., Starast, H., Lindpere, A. 1991. Total phosphorus in Estonian lakes. — *Proc. Estonian Acad. Sci. Ecol.*, 1, 3, 122—130.
- Mäemets, A. (ed.). 1968. Eesti järved. Valgus, Tallinn.
- Mäemets, A. 1974. On Estonian lake types and main trends of their evolution. In: *Estonian Wetlands and Their Life. Estonian Contr. to the IBP*, 7, 29—62.
- Raia, T. 1972. Valguta Mustjärve algofloora. — *Eesti NSV TA Loodusuurijate Seltsi Aastaraamat*, 61, 60—75.
- Timm, T., Kangur, K., Timm, V. 1993. Zoobenthos of some Estonian brown-water lakes. — *Proc. Estonian Acad. Sci. Biol.*, 42, 2, 130—143.
- Глухова В. М. 1979. Личинки мокрецов подсемейств Palpomyiinae и Ceratopogoninae фауны СССР (Diptera, Ceratopogonidae-Helidae). Наука, Ленинград.
- Извекова Э. И., Набережный А. Н., Тодераш И. К. 1983. Питание и пищевые потребности личинок. In: *Мотыль Chironomus plumosus* L. (Diptera, Chironomidae). Наука, Москва, 148—155.
- Кангур К. Э. 1990. Значение мотыля в сукцессии донной фауны дисэвтрофного озера под влиянием минеральных удобрений. In: *Вид в ареале. Биология, экология и продуктивность водных беспозвоночных. Наука і техника, Минск*, 102—105.
- Смирнова Н. Ф., Тимм В. Я., Тимм Т. Э. 1980. Изменения зообентоса. In: *Антропогенное воздействие на малые озера. Наука, Ленинград*, 86—96.
- Тимм Т. (ed.) 1991. Состояние мягководных озер Эстонии. Гидробиологические исследования, 16. АН Эстонии, Тарту.