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THE EFFECT OF FLUCTUATING WATER LEVEL ON THE ZOOPLANKTON OF LAKE VÕRTSJÄRV, CENTRAL ESTONIA

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Abstract. Lake Võrtsjärv (270 km^2) in Central Estonia is a shallow and turbid eutrophic lake with a mean depth of 2.8 m and maximum depth of 6 m. The amplitude of water level fluctuations is large: the annual mean is 1.38 m, annual maximum 2.2 m, and the absolute range 3.2 m. Long-term water level measurements show a periodic alternation of low and high water states within about a 30-year period. In 1996 the water level dropped to the lowest values ever recorded in Lake Võrtsjärv. The annual mean was 1 m lower than the long-term average.

The effect of water level fluctuations on the composition of zooplankton is evident. The amount of zooplankton in the exceptionally low-water year of 1996 was considerably bigger compared with 1995 and 1997. Also, the zooplankton structure characteristic of Lake Võrtsjärv changed in 1996. The percentage of cladocerans increased, whereas that of rotifers decreased. As a result, zooplankton mass increased as well. The causes of changes that occurred in zooplankton lay in changes in phytoplankton, i.e. food for zooplankton. The shallow lake was well illuminated during the ice-free period of 1996 and nutrient enrichment, caused by sediment resuspension, favoured phytoplankton growth. A shift in the species composition from filamentous to chroococcal blue-greens took place and the elevated nutrient level resulted in the formation of a large standing stock of phytoplankton (72 g m^{-3}) in 1996. Small-celled cyanophytes represented an abundant food source for zooplankton, reaching higher biomass and higher mean individual masses in 1996.

Key words: zooplankton, cladocerans, rotifers, water level, shallow lake.

INTRODUCTION

The ecosystem of a shallow lake as well as surrounding areas are strongly affected by large fluctuations of water level in the lake. The low-water period causes an increase in resuspension, accelerates nutrient cycling, and improves illumination of the water column. This leads to massive growth of planktic algae and submerged macrophytes. A low water level causes also winter oxygen depletion due to a significantly lower oxygen storage capacity and a higher amount of easily degradable organic material produced during the vegetation period. Finally, the reed belt expands owing to both vegetative colonization of new shallow regions and generative reproduction occurring in emerging dry areas. These problems have recently arisen in connection with Lake Võrtsjärv, where the lowest water level since 1867 was registered in 1996 (Järvet & Nõges, 1998). An experiment of natural origin has taken place that enables scientists to study the effect of fluctuating water level on certain links of the ecosystem. Making use of this unique opportunity, an investigation was undertaken to analyse the effect of low water level on the composition of zooplankton.

DESCRIPTION OF THE LAKE

Lake Võrtsjärv is a large (270 km^2) shallow (mean depth 2.8 m, maximum depth 6.0 m) eutrophic (N_{tot} about 2 mg N l^{-1} and P_{tot} about 50 µg l^{-1}) lake situated in Central Estonia. Eighteen rivers and streams collect their water from the 3104 km^2 of mostly intensively cultivated drainage basin. A complete turnover of water occurs on average once a year. The water is alkaline (pH 7.5–8.5) with a great buffering capacity. The shallowness of the lake and resuspension of bottom sediments by waves contribute to the development of a high seston concentration and high turbidity of water in summer. During the ice-free period, transparency does not exceed 1 m. The long-term mean level of Võrtsjärv, computed over a 74-year period (1922–96), is 33.64 m according to the Baltic System. The absolute long-term range of level fluctuations is 320 cm, which corresponds to a 93 km^2 difference in the lake area and to 0.874 km^3 difference in its volume. The range of annual water level fluctuations is large, the annual mean being 1.38 m and maximum 2.20 m (Jaani, 1973). Besides seasonal fluctuations, the annual mean water level of dry and rainy years differs by more than one metre. During most of the ice-free period, lake water is well oxygenated. For the first time in a longer than 30-year history of systematic investigations, winter anoxia was registered (in the conditions of low water level) in Lake Võrtsjärv in March 1996 (Nõges et al., 1998).

The recent algal community is represented by an association of filamentous algae: the species of the genus *Aulacoseira* in spring, *Limnothrix redekei*, *L. planctonica*, *Planktolyngbya limnetica*, and *Aphanizomenon skujae* in summer and autumn, accompanied by a low fluctuating biomass of small algae, mostly chlorophytes and chrysophytes. In 1996, the year of extremely low water level, the filamentous species were temporarily replaced by fast growing chroococcal blue-green algae from the genera *Cyanonephron*, *Cyanodictyon*, and *Microcystis* (Nõges & Nõges, 1998). A more specific characterization of the lake is given in the article by Haberman et al. (1998).

MATERIAL AND METHODS

Zooplankton samples were taken with a quantitative Juday net of 85 μm mesh weekly in 1995 and biweekly in 1996 and 1997, samples were taken monthly only in the winter of 1996. The samples were preserved in 4% formaldehyde solution and studied by conventional quantitative analysis (Kiselev, 1956). At least 20 individuals of each species were measured for wet biomass calculation in each sample. Individual masses of rotifers were estimated from average lengths according to Ruttner-Kolisko (1977). Crustacean lengths were converted to weights according to Studenikina & Cherepakhina (1969, nauplii) and Balushkina & Winberg (1979, other groups). Daily water level measurements were performed at the Rannu-Jõesuu Hydrological Station of the Estonian Meteorological and Hydrological Institute.

RESULTS AND DISCUSSION

The mean zooplankton number in 1995–97 was 360,000 ind m^{-3} (S.E. ±51 000, median 199,000) and mean wet biomass, 0.75 g m^{-3} (S.E. ±0.09, median 0.32). Seasonal changes in zooplankton biomass are presented in the Table. The zooplankton biomass of Lake Võrtsjärv was significantly higher in 1996 than in 1995 and 1997 (Fig. 1). The structure of the community was different as well: the share of cladocerans in zooplankton biomass was larger, whereas that of rotifers was smaller (Fig. 2) and mean individual wet mass was larger (Fig. 3) in 1996.

Seasonal averages of zooplankton biomass in Lake Võrtsjärv (g m^{-3})

Year	Winter	Spring	Summer	Autumn
1995	0.03	0.29	1.52	1.45
1996	0.08	1.73	2.34	1.99
1997	0.02	0.49	0.88	0.32

The cause of changes taking place in zooplankton was first of all changes in the food of zooplankton, i.e. phytoplankton, but possibly also decreased fish predation. The shift in phytoplankton was due to the exceptionally low water level in 1996 (Fig. 4).

The long-term mean water level of Lake Võrtsjärv for a period of 74 years (1922–96) is 57 cm above zero water level as recorded at the Rannu-Jõesuu Hydrological Station, or 33.64 m above mean sea level according to the Baltic System (Jaani, 1973; Järvet & Nõges, 1998). Besides seasonal fluctuations,

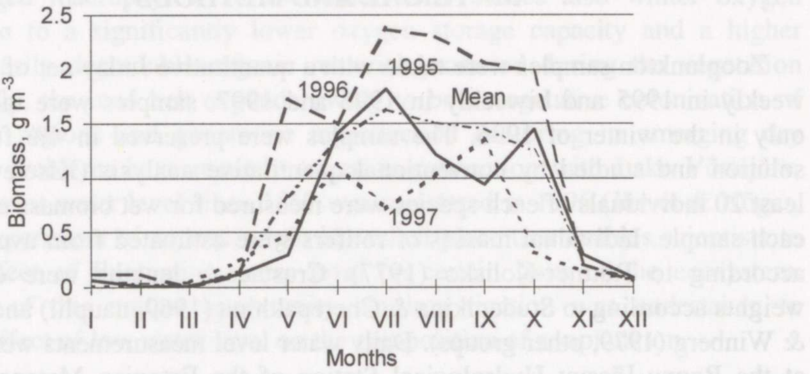

Fig. 1. Wet biomass of zooplankton in Lake Võrtsjärv in 1995–97.

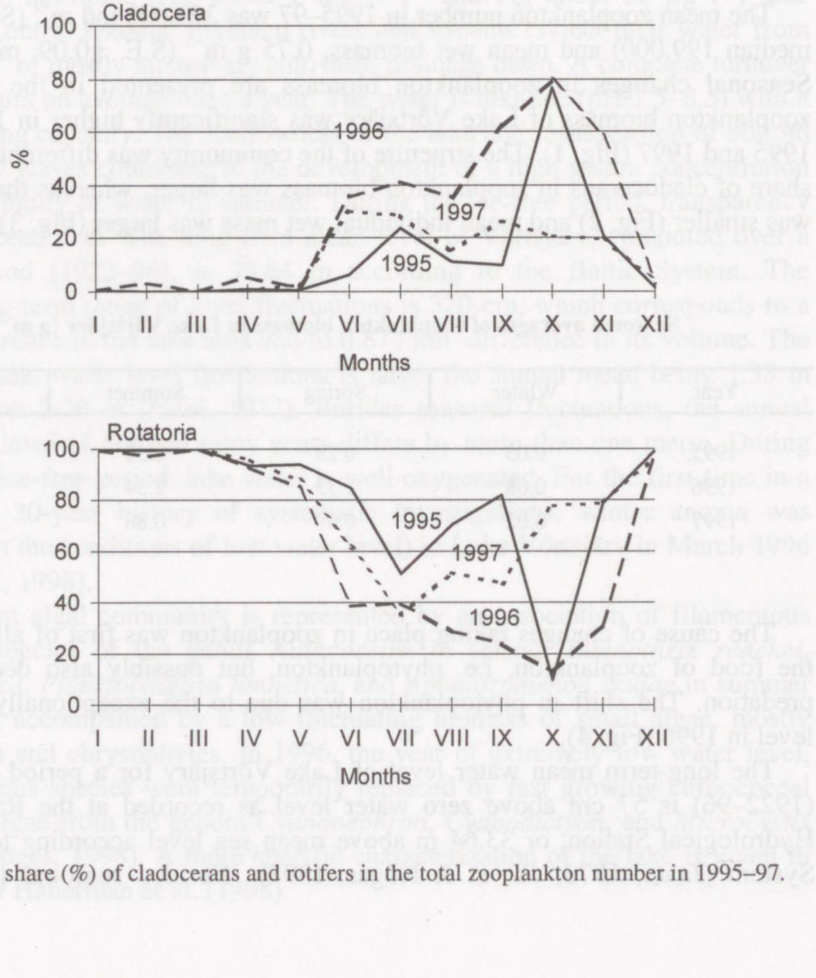

Fig. 2. The share (%) of cladocerans and rotifers in the total zooplankton number in 1995–97.

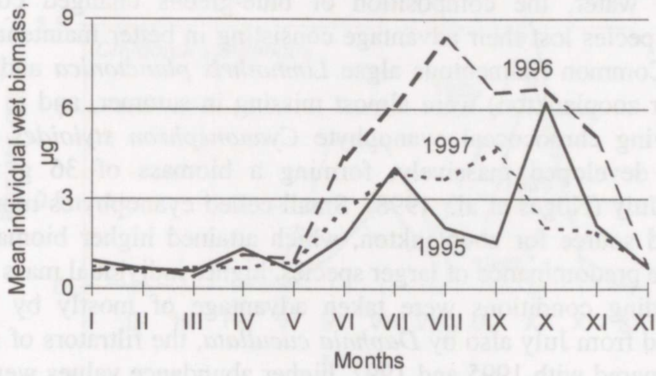

Fig. 3. Mean individual wet mass of zooplankton in Lake Võrtsjärv in 1995–97.

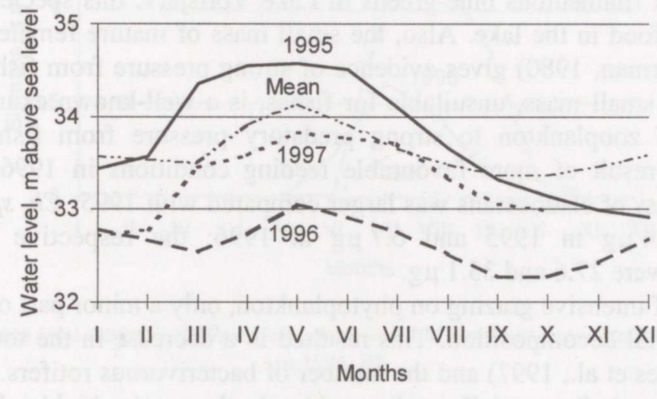

Fig. 4. Fluctuations of water level in Lake Võrtsjärv in 1995–97.

annual mean water level can vary by more than 1.5 m in different years. In 1996, the water level dropped to the lowest values ever recorded in Lake Võrtsjärv. The annual mean level was 43 cm below zero (33.07 m), i.e. 1 m lower than the long-term average (Järvet & Nõges, 1998). Light limitation, which had so far restricted phytoplankton growth, attenuated in 1996. Owing to the low water level, the whole water mass was well illuminated during the ice-free period, which promoted algal growth. Moreover, phytoplankton growth was favoured also by intensive washing-up of sediments by waves and by an increase in the concentration of nutrients, released from them, in shallow water. In the second half of summer, phytoplankton biomass rose up to 72 g m^{-3}, which exceeded the long-term average more than twice (Nõges et al., 1997). Owing to improved light conditions in water, the composition of blue-greens changed considerably. Filamentous species lost their advantage consisting in better maintenance at low light levels. Common filamentous algae *Limnothrix planctonica* and *L. redekei* (nonedible for zooplankton) were almost missing in summer, and in their place the fast growing chroococcal cyanophyte *Cyanonephron styloides* (edible for zooplankton) developed massively, forming a biomass of 36 g m^{-3} at the beginning of July (Nõges et al., 1998). Small-celled cyanophytes represented an abundant food source for zooplankton, which attained higher biomass (Fig. 1) and, due to the predominance of larger species, higher individual mass (Fig. 3).

Better feeding conditions were taken advantage of mostly by *Chydorus sphaericus* and from July also by *Daphnia cucullata*, the filtrators of small algae (Fig. 5). Compared with 1995 and 1997, higher abundance values were observed in the second half of 1996 also in case of other cladocerans (*Bosmina coregoni*, *B. longirostris*, *Alona quadrangularis*, *A. rectangula*, and *A. costata*). The development of *D. cucullata* in Lake Võrtsjärv has always been suppressed, its abundance is low and weight small (Haberman, 1998). Evidently, with the domination of filamentous blue-greens in Lake Võrtsjärv, this species could not find suitable food in the lake. Also, the small mass of mature female specimens (15 µg; Haberman, 1980) gives evidence of strong pressure from fish. Attaining maturity at a small mass, unsuitable for fishes, is a well-known example of the adaptation of zooplankton to strong predatory pressure from fish (Lampert, 1993). As a result of more favourable feeding conditions in 1996, the mean individual mass of cladocerans was larger compared with 1995: *Ch. sphaericus*'s mass was 6.4 µg in 1995 and 6.7 µg in 1996; the respective values for *D. cucullata* were 27.6 and 33.1 µg.

Because of intensive grazing on phytoplankton, only a minor part of algae was left for bacterial decomposition. This resulted in a decrease in the total count of bacteria (Nõges et al., 1997) and the number of bacterivorous rotifers. In summer 1996, *Anuraeopsis fissa* and *Keratella cochlearis*, the species highly characteristic of Lake Võrtsjärv, were nonabundant or lacking. *Polyarthra luminosa*, usually dominating in June and September, had very low abundance in 1996. *Trichocerca rousseleti*, occurring relatively abundantly in summer, was not found in 1996 at all. A major cause of the low abundance of rotifers, besides the shortness of bacteria as their food basis, was also their direct competition with cladocerans. Besides competition for food, cladocerans can suppress the abundance of rotifers also through mechanical elimination. In this case, the effect on rotifers is the stronger the greater is the number of cladocerans and the larger is their size (Pace & Vaqué, 1994; Fussmann, 1996).

The unusually large size of *Chydorus sphaericus* and *Daphnia cucullata* in 1996 represented an advantage for them in this aspect as well. A decrease in the abundance of rotifers could be caused by the growing influence of large predatory ciliates. Recent studies have revealed an important role of protozoans in the lake, among which ciliates have almost the same biomass (~1 g m^{-3}) as crustacean and rotifer zooplankton (Haberman, 1998; Zingel, submitted).

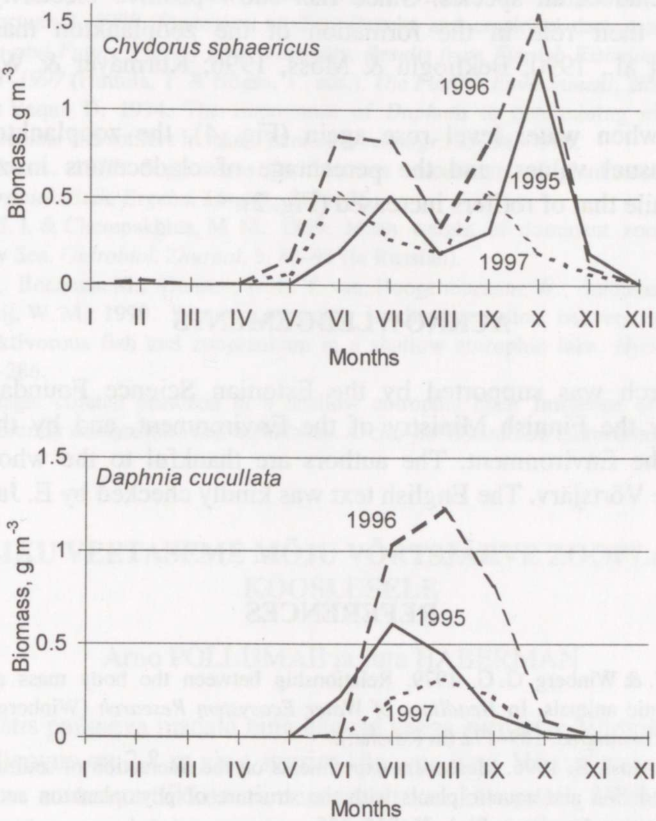

Fig. 5. Biomasses (wet masses) of *Chydorus sphaericus* and *Daphnia cucullata* in Lake Võrtsjärv in 1995–97.

Lake Võrtsjärv is well oxygenated during most of the ice-free period, but the winter of 1995/96 was an example of disastrous consequences of low water level. After the highly productive summer of 1995, the lake was frozen at an extremely low level. The winter was cold and the lake was covered with thick ice (~0.6 m) and snow (~0.3 m). No thawing occurred from December to March, and the lowest oxygen concentration of the 30 years under study was registered in March 1996. At the beginning of March, some oxygen was still left (2.3 mg l^{-1} just below the ice, 0.4 mg l^{-1} in the bottom layer). By mid-March anoxia extended to the whole water column in most parts of the lake (Nõges et al., 1998). Despite the fact that pertaining data are not available, it can be supposed that the abundance of planktivorous juvenile fish decreased by the spring of 1996 as a result of anoxia that had occurred in the lake in March, and hence fish predation decreased as well. An indirect evidence supporting this viewpoint is also an increase in the biomass of cladocerans, favourite food for fish, as well as in the individual mass of different cladoceran species. Since fish show positive electivity for large zooplankters, their role in the formation of the zooplankton mass is great (Vijverberg et al., 1990; Beklioglu & Moss, 1996; Kurmayer & Wanzenböck, 1996).

In 1997, when water level rose again (Fig. 4), the zooplankton biomass restored its usual values, and the percentage of cladocerans in zooplankton decreased, while that of rotifers increased (Fig. 2).

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REFERENCES

Balushkina, E. V. & Winberg, G. G. 1979. Relationship between the body mass and length of planktonic animals. In *Headlines of Water Ecosystem Research* (Winberg, G. G., ed.). Nauka, Leningrad, 169–172 (in Russian).

Beklioglu, M. & Moss, B. 1996. Mesocosm experiments on the interaction of sediment influence, fish predation and aquatic plants with the structure of phytoplankton and zooplankton communities. *Freshwat. Biol.*, **36**, 315–325.

Fussmann, G. 1996. The importance of crustacean zooplankton in structuring rotifer and phytoplankton communities: An enclosure study. *J. Plankton Res.*, **18**, 1897–1915.

Haberman, J. 1980. About the influence of detritus on cladocerans in Lake Võrtsjärv. In *Hydrobiology and Ichtyology of Waterbodies of Estonia. Hydrobiological Researches IX* (Pihu, E., ed.). Tallinn, 52–59 (in Russian).

Haberman, J. 1998. Zooplankton of lake Võrtsjärv. *Limnologica*, **28**, 1, 49–65.

Haberman, J., Nõges, P., Nõges, T., Pihu, E., Kangur, K., Kangur, A. & Kisand, V. 1998. Characterization of Lake Võrtsjärv. *Limnologica*, **28**, 1, 3–11.

Jaani, A. 1973. Hüdroloogia. In *Võrtsjärv* (Timm, T., ed.). Valgus, Tallinn, 37–60.

Järvet, A. & Nõges, P. 1998. Lake water level. In *Present State and Future Fate of Lake Võrtsjärv. Results from Finnish-Estonian Joint Project in 1993–1997* (Huttula, T. & Nõges, T., eds.). *The Finnish Environment*, **209**, 18–21.

Kiselev, J. A. 1956. Methods of plankton research. In *Freshwater Biota of the USSR IV* (Pavlovskij, E. N. & Zhadin, V. I., eds.). Izd. Akad. Nauk SSSR, Moscow, 183–265 (in Russian).

Kurmayer, R. & Wanzenböck, J. 1996. Top-down effects of underyearling fish on a phytoplankton community. *Freshwat. Biol.*, **36**, 599–609.

Lampert, W. 1993. Phenotypic plasticity of the size at first production in *Daphnia*: The importance of matural size. *Ecology*, **74**, 1455–1466.

Nõges, P. & Nõges, T. 1998. The effect of fluctuating water level on the ecosystem of Lake Võrtsjärv, Central Estonia. *Proc. Estonian Acad. Sci. Biol. Ecol.*, **47**, 2, 98–113.

Nõges, P., Haberman, J., Zingel, P., Tammert, H. & Nõges, T. 1997. Võrtsjärve seisund madalaveelisel 1996. aastal. In *Kaasaegse ökoloogia probleemid* (Frey, T., ed.). Tartu, 149–154.

Nõges, T., Nõges, P., Kisand, A., Kisand, V., Tuvikene, L., Zingel, P., Põllumäe, A. & Haberman, J. 1998. Ecological studies. Results and empirical data analysis. In *Present State and Future Fate of Lake Võrtsjärv. Results from Finnish-Estonian Joint Project in 1993–1997* (Huttula, T. & Nõges, T., eds.). *The Finnish Environment*, **209**, 83–112.

Pace, M. L. & Vaqué, D. 1994. The importance of *Daphnia* in determining mortality rates of protozoans and rotifers in lakes. *Limnol. Oceanogr.*, **39**, 985–996.

Ruttner-Kolisko, A. 1977. Suggestions for biomass calculation of planktonic rotifers. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, **8**, 71–76.

Studenikina, E. I. & Cherepakhina, M. M. 1969. Mean weight of dominant zooplankters in the Azov Sea. *Gidrobiol. Zhurnal*, **5**, 89–91 (in Russian).

Vijverberg, J., Boersma, M., Densen, W. L. T. van, Hoogenboezem, W., Lammens, E. H. R. R. & Mooij, W. M. 1990. Seasonal variation in the interaction between piscivorous fish, planktivorous fish and zooplankton in a shallow eutrophic lake. *Hydrobiologia*, **207**, 279–286.

Zingel, P. Pelagic ciliated protozoa in a shallow eutrophic lake: Influence of water level on community composition and abundance. *Archiv für Hydrobiol.* (submitted).

MUUTLIKU VEETASEME MÕJU VÕRTSJÄRVE ZOOPLANKTONI KOOSLUSELE

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Kesk-Eestis paikneva madala ning häguse veega eutroofse Võrtsjärve (270 km^2) keskmine sügavus on 2,8 m ning suurim sügavus 6 m. Võrtsjärvele on iseloomulik veetaseme suur muutlikkus nii sesoonselt kui ka aastati. 1996. aastal registreeriti Võrtsjärve madalaim veetase, mida iial (alates 1867. a.) on mõõdetud. Veetase langes 1 m võrra madalamale paljuaastasest keskmisest. Tekkis suurepärane võimalus uurida veetaseme kõikumise mõju järve elustikule. Selle mõju zooplanktoni kooslusele oli ilmne. Erakordselt madala veega 1996. aastal oli zooplanktonit tunduvalt rohkem kui kõrgema veega 1995. ja 1997. aastal. Ka muutus 1996. aastal Võrtsjärve zooplanktonile iseloomulik struktuur. Kladotseeride tähtsus (%) zooplanktonis suurenes ning keriloomade osa vähenes. Seoses eelnevaga suurenes zooplanktoni keskmine kaal. Zooplanktonis toimunud muutuste põhjuseks olid muutused fütoplanktonis – zooplanktoni toidus. Fütoplanktoni kasvu seni peamiselt piiranud valguslimitatsioon nõrgenes 1996. aastal. Madalast veeseisust tingituna oli jäävabal ajal kogu veemass hästi valgustatud. Madalas vees lainete poolt põhjast ülesuhutud setetest vabanenud biogeenid soodustasid omakorda vetikate arengut, fütoplanktoni biomass tõusis kuni 72 g m^{-3}. Paranenud valgustingimustes toimusid olulised muutused sinivetikate koosluses. Suurenes zooplanktoni toiduks sobivate algsinivetikate ja vähenes mittesobivate niitjate vormide biomass. Paranenud toitumistingimused kasutati ära vetikatoiduliste ning suhteliselt suurte kladotseeride poolt ning sellega suurenes ka zooplanktoni biomass.