BOREAL ENVIRONMENT RESEARCH 3: 251–262
Helsinki 13 November 1998

ISSN 1239-6095

Long-term fluctuations in environmental conditions, plankton and macrophytes in a humic lake, Valkea-Kotinen

Jorma Keskitalo[1], Kalevi Salonen[2] and Anna-Liisa Holopainen[3]

[1] *University of Helsinki, Lammi Biological Station, FIN-16900 Lammi, Finland*
[2] *University of Jyväskylä, P.O. Box 35, FIN-40351 Jyväskylä, Finland*
[3] *University of Joensuu, P.O. Box 111, FIN-80101 Joensuu, Finland*

Keskitalo, J., Salonen, K. & Holopainen, A.-L. 1998. Long-term fluctuations in environmental conditions, plankton and macrophytes in a humic lake, Valkea-Kotinen. *Boreal Env. Res.* 3: 251–262. ISSN 1239-6095

The water of lake Valkea-Kotinen has become acidified to pH ca. 5. In agreement with the decreased deposition of acidifying compounds, the results for 1990–96 indicated no further acidification. However, coverage of the bottom surface by underwater *Sphagnum* moss still increased markedly between 1990 and 1994, possibly due to its slow colonisation and slow recovery of the lake. Phytoplankton primary production, chlorophyll and phytoplankton biomass seemed to respond to factors linked with varying weather conditions. Water inflow from the catchment area and the extent of spring circulation were identified as major factors causing the observed changes. The high dominance of *Gonyostomum semen* (Raphidophyceae) in late summer suggested that, in addition to environmental variables, the behavioural strategies of individual species may also have a strong influence on the diversity and biomass of phytoplankton. Among zooplankton there was a dramatic change in 1993 when a rotifer, *Kellicottia bostoniensis*, suddenly became the most abundant species. This cannot be attributable to the other measured variables and may have been a random occurrence. Overall, the results suggest that 7-year time series may be too short to draw definite conclusions about possible trends. On the other hand the results demonstrated that weekly observations are, in most cases, necessary for finding interrelationships between hydrological and biological factors in small headwater lakes.

Introduction

Continuous biological monitoring of lakes involves much effort and experience in order to reveal causal relationships between changes in environment factors and biological parameters. Consequently only a few long-term biological lake monitoring studies were carried out (e.g., Talling and Heaney 1988, Talling 1993, Gaedke and Schweizer 1993, Sommer *et al*. 1993, Adrian *et al*. 1995). Studies

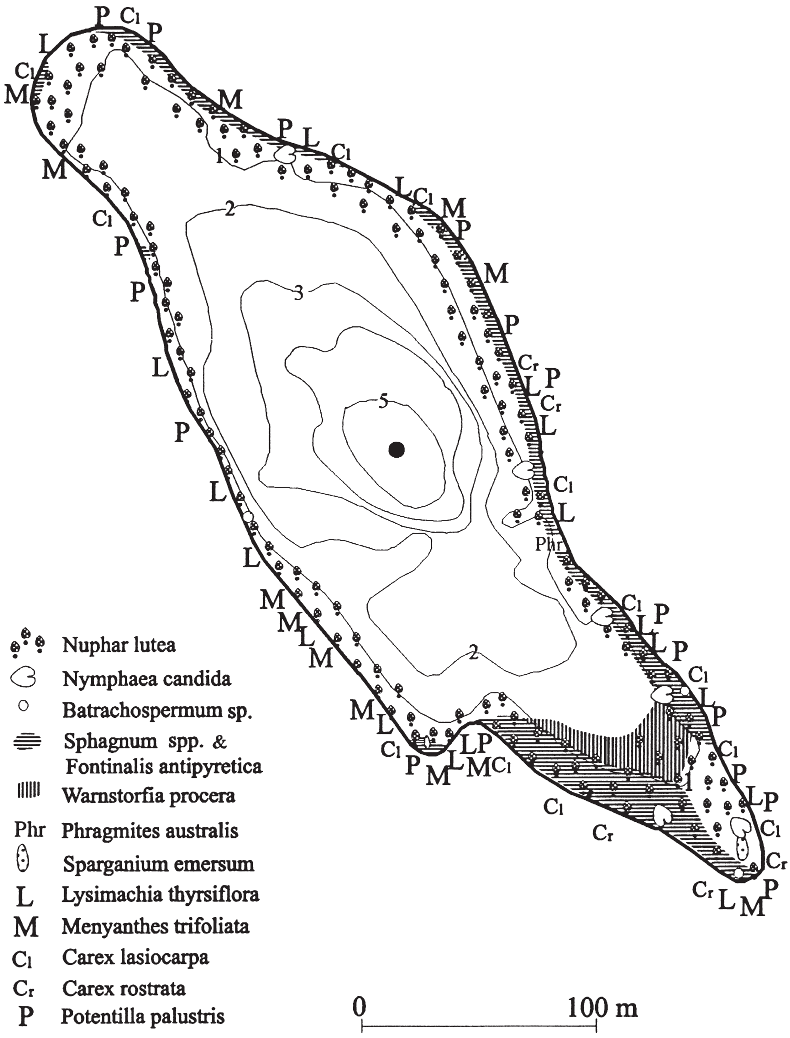

Fig. 1. Depth zones (according to the Geological Survey of Finland), plankton sampling point, and aquatic macrophytes in 1994 in lake Valkea-Kotinen (61°14´N, 25°04´E).

involving dynamic, e.g. primary production, measurements combined with the determination of different plankton assemblages are even more rare.

There are even less long-term biological results from humic lakes than from clear-water lakes. The specific features of small humic lakes in the boreal forest zone are the high attenuation of light (e.g. Eloranta 1978), a shallow epilimnion that results in rapid physico-chemical changes in the epilimnetic water (Smolander and Arvola 1988), and the significant trophic role of allochthonous dissolved organic matter (Salonen *et al.* 1992).

The subprogramme ‘Hydrobiology of lakes’ of the Integrated Monitoring[1] has been carried out in Finland since 1990. Its aim has been to collect data at a frequency which is in a correct relationship with the metabolic activity (i.e. rate of change) of the organisms being studied. Compared to traditional monitoring, this new dimension makes it possible to interrelate changes in the environment with those observed in the biota. Similarly, the high frequency sampling approach allows us to take trophic interactions into account. Furthermore, a high frequency sampling yields more precise estimates of the measured parameters integrated over the whole year. Increased precision of the results, combined with added predictive power from seasonal and episodic cases, should allow the detection of weaker

---

[1] Since 1992 a permanent programme of the United Nations Economic Commission of Europe (UN ECE) by the name ‘International Co-operative Programme on Integrated Monitoring of Air pollution Effects on Ecosystems’.

trends in lake ecosystems and, even more importantly, can yield access to causal relationships.

Water chemistry, plankton metabolism, chlorophyll concentration, phytoplankton and zooplankton densities, macrophytes, benthic fauna and fish were included in the monitoring of a small (4 ha) polyhumic lake, Valkea-Kotinen (Fig. 1), in southern Finland since 1990. This lake is a headwater lake without any significant local pollution and its catchment area has been directly unaffected by man for the past 100 years at least. Hence the lake and its catchment are highly suitable for monitoring the effects of long-range air pollution and climatic change. This paper presents the 7-year results (1990–96) from the hydrobiological monitoring of lake Valkea-Kotinen.

Material and methods

During the ice-free seasons samples were taken weekly in the forenoon, and monthly during winter. Two series of plankton assemblage and chlorophyll samples were taken with a 1-m tube sampler down to a depth of 5 m in the middle of the lake. The samples were pooled to obtain one vertical series. Only one series of samples was taken for the other determinations. The sampling and laboratory procedures were performed according to the optimum programme of the ‘Hydrobiology of lakes’, as described by Keskitalo and Salonen (1994).

Analytical methods for physical and chemical variables were the same as reported by Niinioja *et al.* (1995), and the calculation of heat content and thermal stability of the lake according to Bowling and Salonen (1990).

Primary production was determined using the acidification and bubbling modification of the ^{14}C method (Schindler *et al.* 1972, Niemi *et al.* 1983) with 24 h (48 h in winter) *in situ* incubation. The chlorophyll concentration was determined with a spectrophotometer (at 665 and 750 nm) after extraction of 5 min in hot (75 °C) ethanol. However, 18 h extraction in 4 °C ethanol was used in 1990. The concentration of algal chlorophyll *a* was calculated using an absorption coefficient of 83.4. However, chlorophyll originating from green sulphur bacteria also absorbs at a wavelength of 665 nm, and it proved to be dominant in the anaerobic hypolimnion. The presence of bacteriochlorophyll *d* (maximum absorbance at 654–656 nm) was checked by plotting the absorption spectrum of the sample.

Respiration of plankton was determined *in situ* as the increase in dissolved inorganic carbon (DIC) in dark bottles, and net community production as the respective decrease in DIC in illuminated bottles during 24 h. In winter the incubation time was lengthened (2 d, except for 7 d in January–April 1996) to increase the sensitivity. DIC was determined with a carbon analyser according to Salonen (1981).

Phytoplankton samples were fixed with acid Lugol’s solution. Biomass and species composition were determined with an inverted microscope using a settling chamber technique (Utermöhl 1958). Zooplankton samples were concentrated by pouring water through a 50 µm plankton net, after which the samples were preserved in 4% formaldehyde. Small zooplankton (< 200 µm) was counted in the same way as for phytoplankton. Larger zooplankton was counted under a dissecting microscope in a grooved disk (Hakala 1971).

Results

Changes in the thermal regime and stratification of oxygen

During winter the water layers below 1.5–3 m became anoxic. The oxygen conditions in late winter were somewhat better in 1991–92 than in 1993–96. The maximum thickness of ice was 40–50 cm in March–April, and the ice broke up in late April or early May.

The period of vernal full circulation was often very short and the stratification of temperature developed within a couple of days after the ice break, but in 1995 and 1996 full circulation lasted longer, for ca. two weeks. Vernal circulation generally oxygenated the whole water column, but in 1993 the overturn was incomplete. After thermal stratification oxygen was depleted in the hypolimnion in May–June. The aerobic period in the sediment

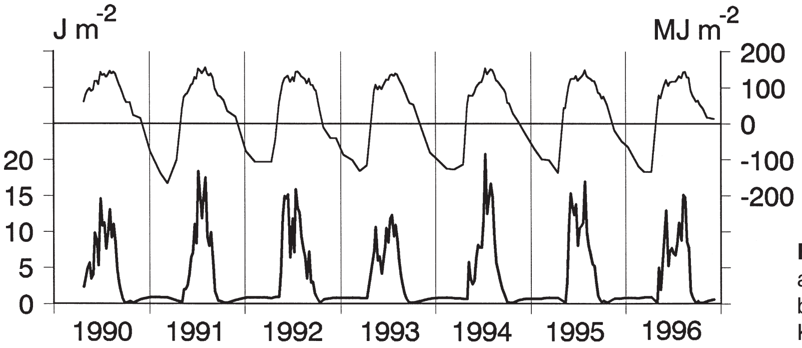

Fig. 2. Heat content (above) and Idso-Schmidt thermal stability (below) in lake Valkea-Kotinen.

of the deepest area lasted for 0–3 weeks during 1990–94, but 6–8 weeks in 1995–96.

In late summer, the epilimnion was shallow (ca. 2 m), and oxygen was depleted in the whole hypolimnion. Anoxia continued until autumnal full circulation, which generally took place in October. Due to the low water temperature, the oxygen concentration then reached ≥ 10 g m^{-3} in the whole water column. The ice cover was formed in October–November (in mid-December in 1996). After the formation of the ice cover, oxygen was gradually depleted in deep water leading to anoxia in November–February. The temperature in the hypolimnion at the time of freezing was always ca. 4 °C.

Heat budget and stability

In winter, the heat content of lake Valkea-Kotinen was strongly negative (Fig. 2), i.e. the mean temperature was < 0 °C when the heat required for the melting of the ice sheet was included. Maximum heat contents in summer were around 150 MJ m^{-2}, with only minor differences between the years. The annual heat budget (difference between maximum and minimum) was highest in 1991 and the mean temperature of the growing season highest in 1992 (Tables 1 and 2). The water temperature reached 24 °C in July 1994, but at the other extreme it remained below 19 °C in summer 1993. However, it must be emphasised that temperature was measured in the forenoon. In the shallow epilimnion, temperature closely followed air temperature. Therefore in summer it was occasionally several degrees higher in the late afternoon than in the forenoon. Water stratification was stable in summer, but varied somewhat between years as shown by the Idso-Schmidt stability index (Fig. 2). The lowest stability was observed in the cold summer of 1993.

Changes in other physical and chemical characteristics

The water of lake Valkea-Kotinen was highly stained by humic substances, which also resulted in a high dissolved organic carbon (DOC) concentration (Table 2) and low Secchi disc transparency (generally 1.4–1.6 m). Reaction of the water was acid and the carbonate buffer system was almost lost in the epilimnion. In late winter and late summer, i.e. towards the end of the stagnation periods, both pH and alkalinity increased in the hypolimnion as a result of sulphate reduction (cf. Cook *et al.* 1986).

Differences in physical and chemical properties between the epi- and hypolimnion were large (Table 2). In early summer, phosphate and nitrate were depleted in the epilimnion and hypolimnion, as well as ammonium in the epilimnion. Later in summer, the phosphate concentration also generally remained below the detection limit in the whole water column, and the nitrate concentration stayed below 15 mg m^{-3} until the autumn circulation. Mean nitrate concentrations were, however, clearly higher in 1996 than in the three previous growing seasons (Table 2). In summer, the DIC concentration was often very low in the epilimnion (minimum < 0.1–0.3 g m^{-3}), while in the hypolimnion it was more than one order of magnitude higher (cf. Table 2).

Epilimnetic DOC and water colour were lower in 1990 than in the later study years (Table 2). The highest colour was observed in 1996. The time series is, however, still too short to determine, whether there is an actual increasing trend or whether the changes are linked with e.g. changes in precipitation (Table 3) and washout into the lake. In 1990, the alkalinity of the epilimnion was negative and only slightly positive in the other years (Table 2). Altogether, no clear trends were evident in the physico-chemical properties during the study period.

Primary production of phytoplankton

In January–February, phytoplankton primary production was very low, 0.1–0.2 mg C m^{-2} d^{-1}. In March it was still ≤1.0 and in April 20–100 mg C m^{-2} d^{-1}. The highest daily production, 210–415 mg C m^{-2} d^{-1}, occurred in May, at the beginning of the ice-free period. Monthly averages tended to decrease from May to early summer and again to increase towards August–September (Fig. 3). In spite of the decrease in illumination, a smaller secondary maximum was observed in 1993 as late as in November after the formation of the ice cover (Fig. 3).

The bulk of primary production was found in the uppermost 0.5–1 m water column and, as a whole, the depth of the productive layer was ≤ 2 m (Keskitalo and Salonen 1998). In spite of the thin productive layer, annual primary production was fairly high, 25–38 g C m^{-2} a^{-1} (Table 4) compared to the other lakes in the area (Arvola 1984). Differences between the years were rather pronounced (Fig. 3).

Net production, as measured as an decrease in DIC in light, was often negative below the depth of 1 m (Keskitalo and Salonen 1998), which shows that decomposition tended to dominate over primary production.

In general, annual primary production correlated poorly with the means of the physico-chemi-

Table 1. Annual heat budget, and stability of the water column of lake Valkea-Kotinen in late summer as calculated with Idso-Schmidt and Birgean indices. θ = heat content, S = Idso-Schmidt stability, B = Birgean wind work (for the calculations, *see* Bowling and Salonen 1990).

Year	Min. θ (MJ m^{-2})	Max. θ (MJ m^{-2})	Max. – Min. (MJ m^{-2})	Max. S (J m^{-2})	Max. B (J m^{-2})
1990		146		14.6	23.8
1991	–166	156	322	18.4	26.5
1992	–107	145	251	15.9	23.3
1993	–132	139	271	12.3	22.2
1994	–128	154	281	20.8	24.7
1995	–137	149	285	17.0	22.8
1996	–134	144	278	15.1	21.6

Table 2. Mean values of physico-chemical properties during the growing season (May–September) for epilimnion (0–1 m) and hypolimnion (3–5 m) in lake Valkea-Kotinen

Variable	Epilimnion							Hypolimnion						
	1990	1991	1992	1993	1994	1995	1996	1990	1991	1992	1993	1994	1995	1996
Water temperature, °C	15.3	15.0	15.8	14.5	15.2	15.1	14.5	7.6	7.5	7.1	6.8	7.2	7.3	6.9
O_2, g m^{-3}	10.0	9.6	9.1	9.5	9.9	8.8	10.1	1.2	2.1	1.6	1.4	1.7	2.5	2.7
pH	5.2	5.4	5.3	5.3	5.3	5.1	5.0	5.3	5.3	5.2	5.3	5.3	5.2	5.3
Conductivity, mS m^{-1}	3.0	2.8	3.1	3.0	2.9	3.1	3.2	3.5	3.2	3.3	3.4	3.1	3.3	3.3
Colour, g Pt m^{-3}	103	128	141	136	140	149	160	154	141	172	178	161	168	157
Total N, mg m^{-3}	462	560	499	436	495	485	475	643	607	678	651	547	682	674
NH_4-N, mg m^{-3}	4	9	12	7	12	25	16	133	89	181	152	74	160	170
NO_3-N, mg m^{-3}	–	–	–	4	5	7	14	–	–	–	6	10	10	24
Total P, mg m^{-3}	19	22	19	18	20	17	15	22	23	22	28	23	23	19
PO_4-P, mg m^{-3}	–	–	–	< 2	< 2	< 2	< 2	–	–	–	< 2	< 2	< 2	< 2
Alkalinity, eq m^{-3}	–0.007	0.009	0.002	0.007	0.011	0.002	0.000	0.054	0.050	0.044	0.068	0.056	0.045	0.051
DIC, g m^{-3}	0.44	0.63	0.64	0.68	0.54	0.88	0.66	–	5.20	4.93	5.95	5.55	5.01	4.54
DOC, g m^{-3}	9.6	11.3	12.2	11.5	11.9	11.4	11.5	–	–	–	–	–	–	–

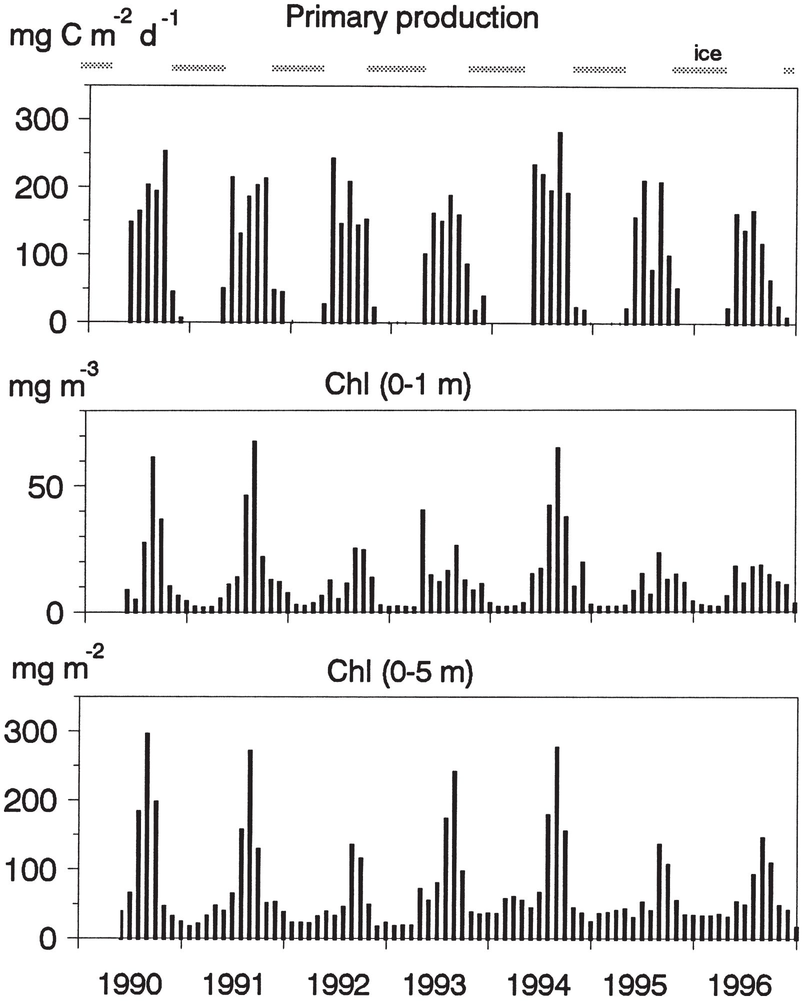

Fig. 3. Monthly means of primary production (above) and chlorophyll concentration in the 0–1-m and 0–5-m water columns in lake Valkea-Kotinen.

cal properties given in Table 2. Significant correlation coefficients were obtained only with epilimnetic DIC (–0.841, $p < 0.05$, $n = 7$), hypolimnetic total nitrogen (–0.853, $p < 0.05$) and hypolimnetic NH_4-N (–0.815, $p < 0.05$).

Chlorophyll concentration

The mean concentration of epilimnetic chlorophyll was at its highest in 1990–91 and 1994 (Table 4). In these years, strong maxima were recorded in

Table 3. Mean air temperature and precipitation during the growing season (May–September) and summer months (June–August) in 1990–96 at Lammi Biological Station 25 km south of lake Valkea-Kotinen.

	1990	1991	1992	1993	1994	1995	1996
Temperature, °C:							
May–September	12.3	12.3	13.7	11.6	12.2	12.8	11.5
June–August	14.2	15.2	15.3	13.2	14.8	15.4	14.0
Precipitation, mm:							
May–September	258	294	268	326	286	293	283
June–August	156	194	193	297	156	151	195

late summer (Fig. 3).

After midsummer the measured chlorophyll values in the hypolimnion were regularly higher than those in the epilimnion. However, the maximum absorbance of hypolimnetic chlorophyll at 654–656 nm instead of 663–665 nm in the epilimnion suggested that anaerobic green sulphur bacteria were the main contributors of hypolimnetic chlorophyll. The late summer bacterial chlorophyll maximum declined rapidly in early autumn, although at this time the concentration of epilimnetic chlorophyll was still high. This was most likely due to the rapid deterioration of the light climate in the autumn.

The epilimnetic chlorophyll concentration correlated significantly with epilimnetic conductivity (–0.829, $p < 0.05$), epilimnetic total P (0.757, $p < 0.05$), hypolimnetic total N (–0.913, $p < 0.01$), and hypolimnetic NH_4-N (–0.944, $p < 0.01$).

Biomass and species composition of phytoplankton

In the years 1990–96, the average growing season biomass of phytoplankton varied between 4.1 and 10.1 g m^{-2} (wet mass). Differences between the years generally followed the differences in primary production, except that biomass was lowest in 1992 and annual production in 1995 (Table 4). In general, a temporary decrease of biomass was observed between spring and late summer. The spring maximum was high in 1993 and the late summer maximum in 1990–91 and 1994 (Fig. 4).

At the time of sampling (forenoon), most of the biomass was found in the uppermost 2 m layer, i.e. in the epilimnion. *Gonyostomum semen* (Raphidophyceae) was most abundant in late summer and formed most of the biomass (Fig. 4). Abundances of the dinophyceans *Peridinium umbonatum, P. lomnickii* and *Gymnodinium* spp. were always highest during spring and late autumn (cf. Dinophyta in Fig. 4). The most abundant chrysophyceans were *Dinobryon bavaricum, D. divergens, Pedinella* spp. and *Uroglena* spp. The cryptophyceans, *Cryptomonas* spp., were very common in 1993 and 1995, and the diatom *Asterionella ralfsii* var. *americana* in 1990 and in 1993.

Phytoplankton biomass (0–5 m) correlated significantly only with hypolimnetic total N (–0.883, $p < 0.01$) and hypolimnetic NH_4-N (–0.860, $p < 0.01$). The ammonium nitrogen concentration was low in the hypolimnion during the maximum biomass of *Gonyostomum semen*, especially in 1994.

Respiration of plankton

With the exception of 1995–96, community respiration during the growing season in the 0–2 m water column was on the average somewhat higher than the primary production (Table 4). The seasonal variations of respiration followed those of primary production and the chlorophyll concentration, though they were not always exactly simultaneous. For instance, in 1996 the respiration maxima occurred in June and August, while the

Table 4. Mean values of biological variables in the growing season (May–September) in 1990–96. Annual primary production is an integrated value for the whole year.

	1990	1991	1992	1993	1994	1995	1996
Primary production, mg C m^{-2} d^{-1}	189	188	177	147	223	145	170
Annual production, g C m^{-2} a^{-1}	36	33	28	28	38	25	28
Net production, mg C m^{-2} d^{-1} (0–2 m)	–	–	47	45	90	46	64
Respiration, mg C m^{-2} d^{-1} (0–2 m)	205	222	192	194	233	135	158
Chlorophyll concentration, mg m^{-3} (0–1 m)	27	31	15	16	35	13	15
Phytoplankton, wet biomass g m^{-2} (0–5 m)	8.7	7.2	4.1	6.1	10.1	4.6	5.1
Protozooplankton, wet biomass mg m^{-2} (0–5 m)	440	290	280	501	377	243	240
Zooplankton*, 10^3 ind. m^{-2} (0–5 m)	2 234	2 372	4 140	9 295	7 525	8 535	
Cladocera, 10^3 ind. m^{-2} (0–5 m)	85	112	64	37	41	64	
Copepoda, 10^3 ind. m^{-2} (0–5 m)	157	112	130	405	201	363	
Rotatoria, 10^3 ind. m^{-2} (0–5 m)	1 992	2 148	3 946	8 853	7 283	8 109	

* Protozooplankton excluded. Results for 1996 not yet available.

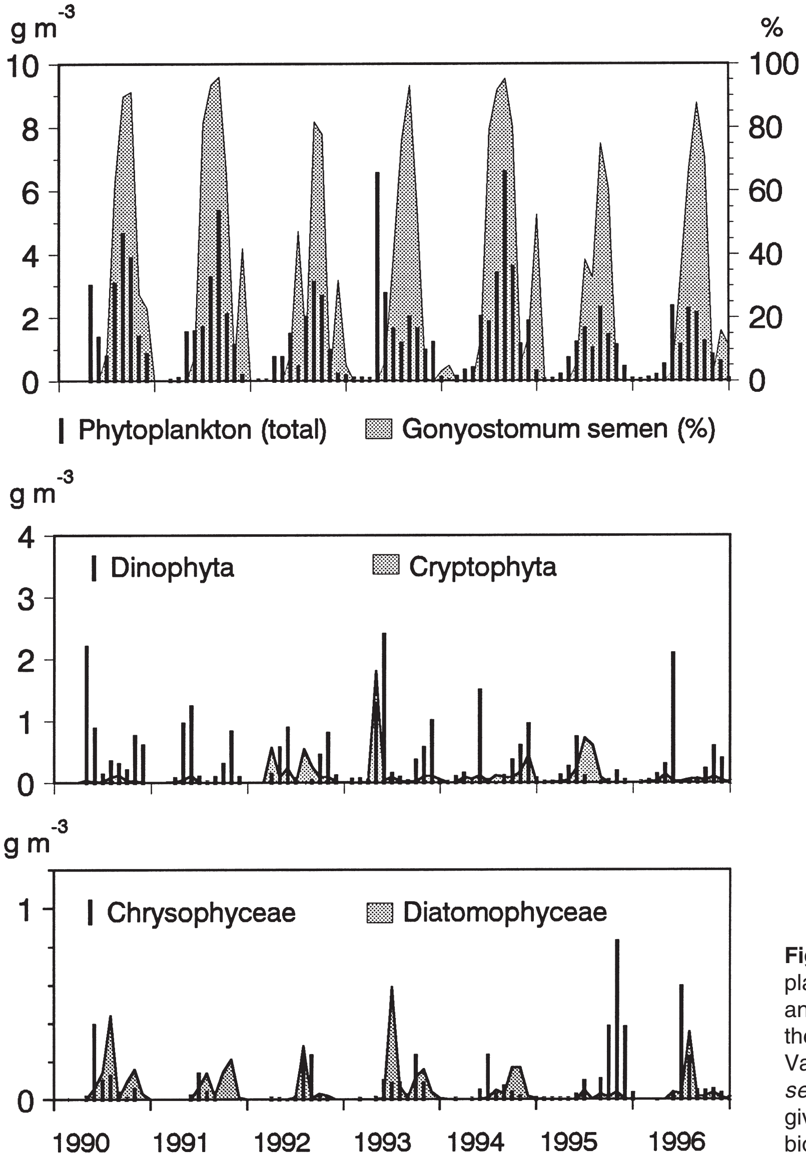

Fig. 4. Monthly means of phytoplankton biomass (wet mass) and some important groups in the 0–1-m water column in lake Valkea-Kotinen. *Gonyostomum semen* (Raphidophyceae) is given as a percentage of total biomass.

maxima of primary production and chlorophyll concentration were reached already in May and in July–August.

Density and species composition of zooplankton

In the zooplankton of lake Valkea-Kotinen rotifers dominated in numbers (Table 4). The most abundant rotifers were *Keratella cochlearis, K. ticinensis, Polyarthra vulgaris* and *Asplanchna priodonta*. The most prominent change during the study period was a drastic increase of *Kellicottia bostoniensis*. Only a few *K. bostoniensis* individuals were found in 1990–91, but it later became the dominant rotifer species. Its increase was almost solely responsible for the increase in total zooplankton density in Valkea-Kotinen during the study period (Fig. 5, cf. Table 4). Copepods were present in all seasons. In 1993–95 (results for 1996 not yet available), they had a rather high maximum in July–August. The most important copepods were *Mesocyclops leuckarti* and *Thermo-*

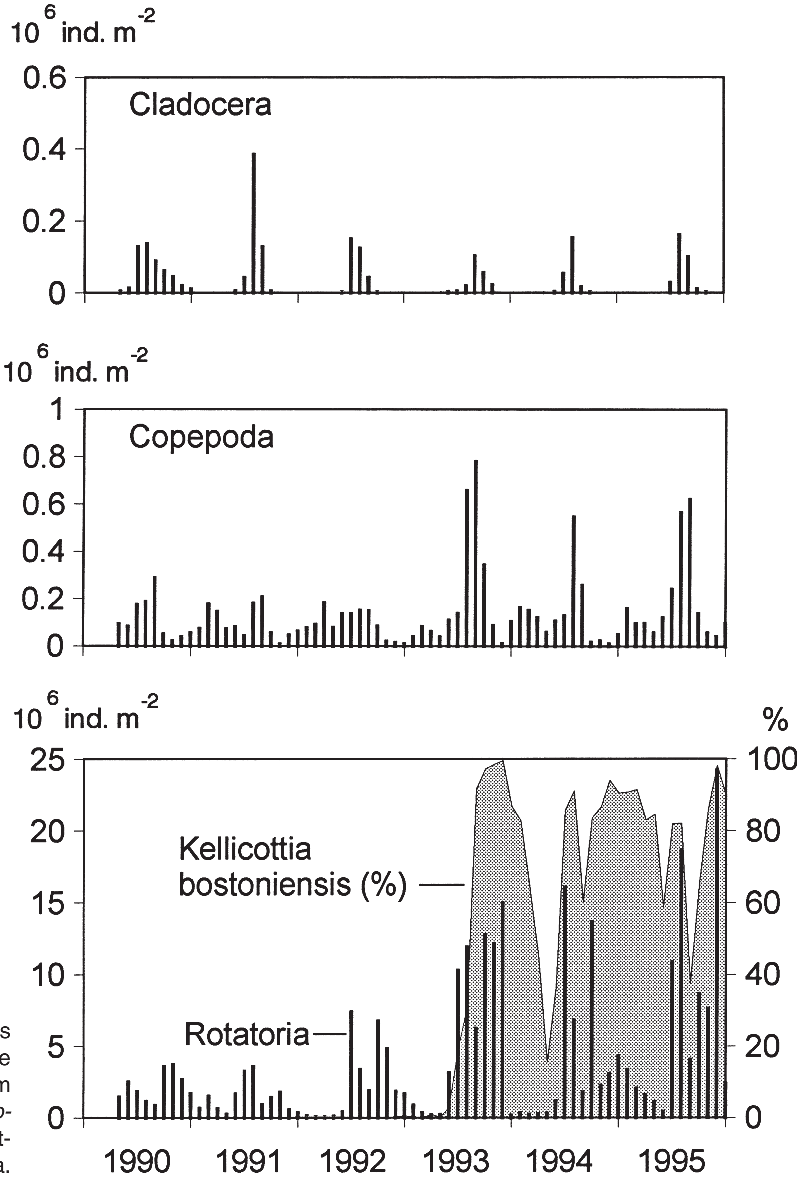

Fig. 5. Monthly mean densities of zooplankton groups in lake Valkea-Kotinen in the 0–5-m water column. *Kellicottia bostoniensis* is given as a percentage of total density of Rotatoria.

cyclops spp. The occurrence of cladocerans was restricted mainly to the summer (Fig. 5), and the most abundant species were *Holopedium gibberum*, *Bosmina longirostris* and *Ceriodaphnia quadrangula* (maximum of the last mentioned species on 23 July 1991, 0.54 × 10^6 ind. m^{-2}).

Aquatic macrophytes

The most common shore plants (occurring at the shore-line or just above it) were the vascular plants *Andromeda polifolia*, *Carex lasiocarpa*, *C. rostrata*, *Lysimachia thyrsiflora*, *Peucedanum palustris*, *Potentilla palustris*, and the bryophytes *Sphagnum fallax* and *S. flexuosum* (cf. Fig. 1). No changes in the occurrence of these plants were observed during the study period.

The shore of Valkea-Kotinen drops directly from the shoreline to a depth of 0.2–0.7 m. The steepness, mud bottom and high water colour restrict the occurrence of aquatic macrophytes in Valkea-Kotinen. The biomass consisted mainly of *Nuphar lutea* and of the submerged bryophytes

Sphagnum spp. and *Warnstorfia procera* (Table 5). There were also some *Nymphaea candida, Sparganium emersum, Phragmites australis* (vascular plants), *Fontinalis antipyretica* (bryophyte) and *Batrachospermum* sp. (red alga) (Fig. 1). Submerged vascular plants were missing, and the depth limit of the vegetation was 1.6 m. The highest coverage of the stands of submerged *Sphagnum* was 35% in the shallow SE bay in 1990, but > 80% in 1994.

Discussion

The epilimnion of lake Valkea-Kotinen is acid and its carbonate buffering system against acidification is almost completely lost. The heavily coloured water reduces light penetration, although its effects on phytoplankton may have been overcome by the fact that the most abundant algal species are motile. Further, several factors restrict the input of nutrients to Valkea-Kotinen: it is a headwater lake, located within one of the most pristine areas in Southern Finland, and its catchment area is small (30 ha). However, the annual primary production of Valkea-Kotinen was high (25–38 g C m^{-2} a^{-1}) compared with its neighbouring polyhumic lakes (both with anoxic hypolimnion) Horkkajärvi and Nimetön (ca. 6 g C m^{-2} a^{-1} ; Arvola 1983).

The mechanism of the high production in Valkea-Kotinen seems to be linked to the vertical migrations of flagellated algae (*Gonyostomum semen, Cryptomonas*). The flagellates move down into the anaerobic hypolimnion at night to take nutrients and, in the morning, they migrate back into the epilimnion (Salonen *et al.* 1993; Salonen and Rosenberg, unpublished). This would explain the relatively low production, chlorophyll concentration and phytoplankton biomass in 1995–1996. In these years the spring circulation lasted for an extended period and, consequently, the nutrient flux from the anaerobic sediment was delayed. This does not, however, explain the fairly low production in 1993, when spring circulation did not reach the bottom at all. One of the most remarkable signs of the importance of vertical migration was the exhaustion of the nutrient supply in the hypolimnion in 1994 (K. Salonen and M. Rosenberg, unpubl.).

In general, variations in the mean values of physical and chemical variables did not satisfactorily explain the year-to-year variations in primary production, epilimnetic chlorophyll concentration and in the phytoplankton assemblage. In fact, production, phytoplankton biomass and algal chlorophyll correlated negatively with hypolimnetic total nitrogen and hypolimnetic ammonium nitrogen, which is at first sight surprising. One reason for this may be the more thorough utilisation of nutrients during those growing seasons when primary production was high and a large biomass of migrating algae developed. The time series is, however, probably still too short to include an adequate range of variation and combinations of random phenomena.

The diatom flora in the bottom sediments indicates that up until the early 1970s the pH was about one pH-unit higher than during the study period (Liukkonen 1989). Thus Valkea-Kotinen has become acidified but, during this study, there was no sign of further acidification since 1990. This may be due to the decreasing deposition of acidifying compounds in southern Finland since the 1980s (Leinonen 1994). Another explanation might have been the increased generation of alkalinity by sulphate reduction in the anoxic hypolimnion. Although only the first year of our time series indicated negative alkalinity, it may

Table 5. Estimated stand areas and above-ground biomasses of aquatic macrophytes in lake Valkea-Kotinen in late summer 1994. Plants occurring at the shore-line are excluded.

Taxon	Area (m^2)	Wet mass (kg)	Dry mass (kg)
Bryophyta	3 600	4 637	205
Nuphar lutea	15 400	961	144
Nymphaea candida	–	8	1
Phragmites australis	10	6	2
Sparganium emersum	46	24	2
Total		5 628	353

be linked to the markedly lower colour of the water compared to the other years. The higher load of DOC since 1990 may have increased anoxy and sulphate reduction to such an extent that it was reflected as a cessation of further acidification. The only indication of a continuing acidification process was the increase of submerged *Sphagnum* spp. (cf. Farmer 1990, Heitto 1990) in the early 1990s, but this may be due to the fact that the response of macrophytes is rather slow compared with e.g. phytoplankton.

The densities of zooplankton individuals increased during the study period due to a drastic increase of the rotifer *Kellicottia bostoniensis*, but the reason for this remains uncertain. *K. bostoniensis* is a North American species, which was observed for the first time in Finland in 1987 by Eloranta (1988). It may also have only randomly invaded Valkea-Kotinen.

In general, the results showed significant differences between successive years. However, within the 7-years time series it generally proved difficult to find explanations for most of the observed differences and even less so for complex chains of causes and consequences. Any reasonable statistical approach to reveal trends would most likely need a time series at least two times longer. Biological results also often include random variation, which also necessitates even longer time series. Thus it may be concluded that the monitoring of Valkea-Kotinen is still entering a really productive stage and its usefulness is now increasing rapidly. Further, although this type of monitoring with a good coverage of the whole ecosystem can be considered expensive, even in systems as simple as Valkea-Kotinen it is the most likely form of monitoring able to answer future unforeseen questions.

Acknowledgements: The study was financed by the Finnish Ministry of the Environment. Lammi Biological Station provided working facilities. Our thanks are due to Anja Lehtovaara, Anne Ojala, Tarja Rousku and Tuija Sohlberg for the microscope work on the zooplankton samples, and to Jaakko Vainionpää and Riitta Ilola for handling and analysing the chemical and physical samples. Nutrient samples were determined by the Uusimaa and Häme Regional Environment Centres. The staff of the Lammi Biological Station, as well as that of the Evo Forestry School and of the Evo Fisheries Research, assisted in the field work. John Derome revised the English of the manuscript.

References

Adrian R., Deneke R., Mischke U., Stellmacher R. & Lederer P. 1995. A long-term study of the Heiligensee (1975–1992). Evidence for the effects of climatic change on the dynamics of eutrophied lake ecosystems. *Arch. Hydrobiol.* 133: 315–337.

Arvola L. 1983. Primary production and phytoplankton in two small, polyhumic forest lakes in southern Finland. *Hydrobiologia* 101: 105–110.

Arvola L. 1984. Vertical distribution of primary production and phytoplankton in two small lakes with different humus concentration in southern Finland. *Holarct. Ecol.* 7: 390–398.

Bowling L. & Salonen K. 1990. Heat uptake and resistance to mixing in small humic forest lakes in southern Finland. *Aust. J. Mar. Freshwater Res.* 41: 747–759.

Cook R. B., Kelly C. A., Schindler D. W. & Turner, M. A. 1986: Mechanisms of hydrogen ion neutralization in an experimentally acidified lake. *Limnol. Oceanogr.* 31: 134–148.

Eloranta P. 1978. Light penetration in different types of lakes in Central Finland. *Holarct. Ecol.* 1: 362–366.

Eloranta, P. 1988. *Kellicottia bostoniensis* (Rousselet), a planktonic rotifer species new to Finland. *Ann. Zool. Fennici* 25: 249–252.

Farmer A. M. 1990. The effects of lake acidification on aquatic macrophytes — a review. *Environ. Pollut.* 65: 219–240.

Gaedke U. & Schweizer A. 1993. The first decade of oligotrophication in Lake Constance. I. The response of phytoplankton biomass and cell size. *Oecologia* 93: 268–275.

Hakala I. 1971. A new model of the Kajak bottom sampler, and other improvements in the zoobenthos sampling technique. *Ann. Zool. Fennici* 8: 422–426.

Heitto L. 1990. Macrophytes in Finnish forest lakes and possible effects of airborne acidification. In: Kauppi P., Kenttämies K. & Anttila P. (eds.), *Acidification in Finland*, Springer-Verlag, Berlin, Heidelberg, pp. 963–972.

Keskitalo J. & Salonen K. 1994. Manual for Integrated Monitoring. Subprogramme hydrobiology of lakes. National Board of Waters and the Environment, Helsinki, *Publications of the Water and Environment Administration* B 16: 1–41.

Keskitalo J. & Salonen K. 1998. Fluctuations of phytoplankton production and chlorophyll concentrations in a small humic lake during six years (1990–1995). In: George D.G., Jones J.G., Punčochář P., Reynolds C.S. & Sutcliffe D.W. (eds.), *Management of lakes and reservoirs during global climate change*. Kluver Academic Publishers, pp. 93–109.

Leinonen L. (ed.) 1994. *Ilmanlaatumittauksia — Air quality measurements 1993*. Finnish Meteorological Institute, Helsinki. 245 pp. [In Finnish and English].

Liukkonen M. 1989. *Latvajärvien happamoituminen Suomessa sedimentoituneen piilevästön osoittamana.*

M.Sc. Thesis, Dept. Bot., Univ. Helsinki, 147 pp. + appendices.

Niemi M., Kuparinen J., Uusi-Rauva A. & Korhonen K. 1983. Preparation of algal samples for liquid scintillation counting. *Hydrobiologia* 106: 149–156.

Niinioja, R., Villa, L., Ylitolonen, A. & Mähönen, O. 1995. Material and methods. Water chemistry. In: Bergström I., Mäkelä K. & Starr M. (eds.), *Integrated Monitoring Programme in Finland. First National Report*. Ministry of the Environment, Environmental Policy Department, Helsinki. Report 1: 39.

Salonen K. 1981. Rapid and precise determination of total inorganic carbon and some gases in aqueous solutions. *Water Res.* 15: 403–406.

Salonen K., Arvola L. & Rosenberg M. 1993. Diel vertical migrations of phyto- and zooplankton in a small steeply stratified humic lake with low nutrient concentration. *Verh. Internat. Verein. Limnol.* 25: 539–543.

Salonen K., Arvola L., Tulonen T., Hammar T., Metsälä T.-R., Kankaala P. & Münster, U. 1992. Planktonic food chains of a highly humic lake. I. A mesocosm experiment during the spring primary production maximum. *Hydrobiologia* 229: 125–142.

Schindler D.W., Schmidt R.V. & Reid R.A. 1972. Acidification and bubbling as an alternative to filtration in determining phytoplankton production by the ^{14}C method. *J. Fish. Res. Bd. Canada* 29: 1627–1631.

Smolander U. & Arvola L. 1988. Seasonal variation in the diel vertical distribution of the migratory alga Cryptomonas marssonii (Cryptophyceae) in a small, highly humic lake. *Hydrobiologia* 161: 89–98.

Sommer U., Gaedke U. & Schweizer A. 1993. The first decade of oligotrophication of Lake Constance. II. The response of phytoplankton taxonomic composition. *Oecologia* 93: 276–284.

Talling J. F. 1993. Comparative seasonal changes, and inter-annual variability and stability, in a 26-year record of total phytoplankton biomass in four English lake basins. *Hydrobiologia* 268: 65–98.

Talling J. F. & Heaney S. I. 1988. Long-term changes in some English (Cumbrian) lakes subjected to increased nutrient inputs. In: Round F. E. (ed.), *Algae and the aquatic environment*. Biopress, Bristol, pp. 1-29.

Utermöhl H. 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitt. Internat. Verein. Limnol.* 9: 1–38.

Received 2 March 1998, accepted 10 July 1998