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Responses of zooplankton to long-term environmental changes in a small boreal lake

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Zooplankton dynamics were examined in a small boreal lake over a 20-year period and interpreted in relation to climate change, brownification and recovery from acidification. Significant changes were recorded in the abundance of dominating crustacean species but not of rotifer species. According to redundancy analysis (RDA), the long-term pattern in crustacean zooplankton was mainly associated with abiotic factors like water colour, alkalinity and total phosphorus. Primary production of phytoplankton was the most important biological parameter whereas planktivorous perch and *Chaoborus* larvae had a marginal contribution. Biological factors were relatively more important for rotifers than for crustaceans, primary production being the most powerful explanatory parameter, followed by alkalinity, total phosphorus and colour. The changes in the zooplankton community were mainly related to increased organic carbon load and recovery from acidification. Within the food web, bottom-up regulation seemed to exceed the importance of top-down control.

Introduction

During the last two decades boreal headwaters experienced environmental changes. Until the end of the 1980s, long-range transport of sulphur and nitrogen oxides caused widespread acidification of aquatic ecosystems (Schindler 1988, Rodhe *et al*. 1995). Successful reduction of SO_2 emissions by e.g., 73% in Europe during 1990–2009 (Fagerli *et al*. 2011, *see* also Ruoho-Airola *et al*. 2014), resulted in chemical and biological recovery of acidified lakes (Stoddard *et al*. 1999, Skjelkvåle *et al*. 2005). In northern European and North American lakes this has led to an increase in allochthonous dissolved organic carbon (DOC) load (Vuorenmaa *et al*. 2006, Monteith *et al*. 2007). Today, climate change due to increased emissions of greenhouse

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gases and consequent global warming is considered a major environmental threat (Root *et al* 2003) also affecting aquatic ecosystems (Heino *et al*. 2009, Jeppesen *et al*. 2012, MacLennan *et al*. 2012). Climate change induced alterations in hydrological conditions also contribute to brownification of lakes (Futter *et al*. 2009).

Increasing organic carbon increases water colour and hence it limits light penetration which in small lakes affect thermal and oxygen stratification (Forsius *et al*. 2010, Vuorenmaa *et al*. 2014). Decreased light penetration reduces the thickness of the layer where phytoplankton primary production is possible (Arvola *et al*. 2014). At higher trophic levels, visually feeding fish like perch (*Perca fluviatilis*) suffer from poor light conditions and decrease foraging efficiency (Bergman 1988, Estlander *et al*. 2012). Because zooplankton is affected by both top-down and bottom-up processes (Persson *et al*. 1988, Carpenter *et al*. 2001), they may be affected by changes in the availability of food or in predation by fish or invertebrates (Järvinen and Salonen 1998, Järvinen 2002). Further, DOC may contribute significantly to energy and carbon sources and processes within food webs of both humic (Salonen *et al*. 1992, Kankaala *et al*. 2006, Jones *et al*. 2008) and clear-water lakes (Ask *et al*. 2009, Karlsson *et al*. 2009), and may lead to poorer quality of food for zooplankton due to limited availability of essential fatty acids (Brett *et al*. 2009). Recently, Palmer and Yan (2013) showed evidence that individual and combined impacts of multiple anthropogenic stressors such as changes in water quality, climate and invasion of an exotic predator have caused regional-scale changes in zooplankton over decades. Their findings highlight the complexity of ecosystem responses to multiple stressors.

Long-term data sets have proven useful to reveal causal relationships in lakes where physical, chemical and biological properties are more or less randomly combined (Magnuson *et al*. 2004, 2006), or when environmental conditions have changed, for instance, as a result of eutrophication or climate warming (Schindler 2009). Such data may be especially valuable if changes in lake ecosystems with irregular or cyclic fluctuations are interpreted (e.g. Talling and Heaney 1988, Gaedke and Schweizer 1993, Adrian *et al*. 1995).

In this paper, we present patterns in the dynamics and composition of the zooplankton community as related to long term environmental changes in Lake Valkea-Kotinen, a small pristine acidic and humic lake in southern Finland. The lake and its catchment have been studied intensively since 1990 as a part of the International Co-operative Programme on Integrated Monitoring of Air Pollution Effects on Ecosystems (UNECE ICP IM, *see* Rask *et al*. 1998, and other papers in this issue). We address the following three questions: Is there any change in the long-term and seasonal occurrence of zooplankton? How has the zooplankton community responded to long-term environmental changes? And what is the role of other biota in zooplankton responses?

Material and methods

Lake Valkea-Kotinen is a polyhumic, small and shallow headwater lake (water colour > 100 Pt mg l^{-1}, area 0.042 km^2, mean depth 2.5 m, maximum depth 6.5 m) which is located in the Kotinen State Reserve (61.24232 N, 25.06266 E) in Hämeenlinna, Finland (Vuorenmaa *et al*. 2014). The epilimnion where photosynthesis of phytoplankton occurs is only 1.5–2 m thick (Forsius *et al*. 2010, Arvola *et al*. 2014), and the hypolimnion is anoxic during stratified periods. The littoral vegetation zone consists of only few macrophytes growing in the boundary layer between soil and water, as well as a floating-leaved vegetation and aquatic mosses on the bottom of the lake. According to surveys carried out by Keskitalo and Heitto (1996) and M. Partanen (unpubl. data) the coverage of the higher macrophyte vegetation was 37% of the bottom surface in 1990s and 29% in 2012, and including the bryophytes on the bottom 45% and 57%, respectively. Perch and pike (*Esox lucius*) are the only fish species present in the lake (Rask *et al*. 1998). The population dynamics and growth of perch has been studied extensively since 1990 (Rask *et al*. 1998, 2014).

Chemical monitoring of the lake has been carried out by Finland's Environmental Administration (Finnish Environment Institute and Centre for Economic Development, Transport and the

Environment for Häme) and Lammi Biological Station, University of Helsinki. The monitoring of air pollution has been carried out by Finland's Environmental Administration with seasonal sampling. Water samples were taken monthly in March–August, and once in October and December from depths of 1, 3 and 5 m. Weekly nutrient and carbon samples at 1-m intervals from 0 m to 6 m were taken during May–October by the staff of the Lammi Biological Station (*see* Keskitalo *et al*. 1998, Arvola *et al*. 2014). All samples were taken with Limnos tube samplers at the site of maximum depth in the middle of the lake and analyzed using standard methods (*see* Vuorenmaa *et al*. 2014). Temperature and oxygen were measured weekly during the ice-free period from May to October at 1-m intervals using YSI 55 combined temperature-oxygen meter (Yellow Springs Instruments Inc., Yellow Springs, OH, USA).

Primary production and biomass of phytoplankton were measured during the open-water period (from mid-May until the end of September). The sampling time (approx. 11:00) was constant throughout the study. Composite water samples were from three lifts of a 0.3-m long Limnos tube sampler (2.8 l) taken from around the boat (*see* details in Arvola *et al*. 2014). Primary production was determined using acidification and bubbling modification of the ^{14}C-method (Schindler *et al*. 1972). Biomass and species composition were determined with an inverted microscope using a settling chamber technique (Utermöhl 1958). For more details, *see* Peltomaa *et al*. (2013) and Arvola *et al*. (2014).

Zooplankton samples were taken with a 1-m-long tube sampler (6.7 l) every second week during the open-water period (from mid-May until the end of September) from the deepest point of the lake. Similar to other measurements, the sampling time was constant. Two parallel samples were combined from the surface down to 5-m depth at 1-m intervals, resulting in a 67 liter total volume sample. Sample water was sieved through a 50 μm plankton net, washed into a 250 ml polyethylene bottle and preserved with a formaldehyde solution (final concentration 4%). In the laboratory, each sample was divided into two equal parts one of which was combined with respective other samples to get 0–5 m composite samples which were used in the present study.

Rotifers were counted with an inverted microscope (Wild M40 with phase contrast) at 100× magnification, and copepods and cladocerans by using a dissecting microscope (Olympus SZH10 Research Stereo) with 10–50× magnification. For identification, higher magnification was used, and for counting both plankton cuvettes and grooved plates were applied. Usually all crustaceans from a sample were counted, and a minimum of 200 individuals of the most common species in the cases when subsamples had to be taken from abundant samples. For rotifers, subsampling was used more regularly, still keeping the principle of 200 counted individuals of the most abundant species. The organisms were identified to species or genus level whenever possible. *Chaoborus* larvae were also counted from the zooplankton samples.

The population size, length frequency distribution and growth of perch were monitored throughout the 20-year study period. Population estimate (Schnabel, multiple marking, Krebs 1989), and relative year class strength of 0–3-year-old perch were used in analyzing the potential effects of perch predation on zooplankton. The latter was derived from occurrence of perch of different year-classes in annual samples (50–100 perch) added with the effect of a mortality estimate (0.6, Thorpe 1977) for 0+ and 1+ perch. For more detailed methods, *see* Rask *et al*. (1998, 2014).

Seasonal Kendall's test — henceforth SK — (Hirsch *et al*. 1982; *see* also Vuorenmaa *et al*. 2014) was used for detecting long-term trends in water chemistry. The long-term trends were calculated for samples taken from the depth of 1 m or integrated 0–1 m samples for the period 1990–2009. The slope of the trend was calculated with Sen's slope estimation method (Sen 1968). Trends in zooplankton groups and species were tested using a Mann-Kendall test — henceforth MK — (*see* Hipel and McLeod 2005).

To analyse the joint effects of abiotic and biotic (i.e. environmental) factors on the yearly mean abundances of zooplankton species, a redundancy analysis (RDA, Canoco 4.51; ter Braak and Šmilauer 2002) was applied. RDA was chosen as a multivariate analysis method, because the gradient lengths of biotic variables were rather short, ca. 4 SD units. Due to the low sample sizes, the analyses were done separately for the most abundant crustacean zooplankton species and Cyclopoida nauplius and for planktonic rotifers species. The explanatory environmental and abiotic factors were selected according to the automatic forward selection procedure (based on maximum extra fit; ter Braak and Šmilauer 2002). Before the forward selection procedure, in order to reduce the risk for multicollinearity, oxygen concentration (at 2 m depth) and pH were excluded due to their high correlation (≥ |0.6|) with several other environmental variables. The standardized $[(x_i - x_{mean})SD^{-1}]$ abiotic and biotic variables included in the forward selection procedure were temperature, Gran alkalinity (alkalinity), total phosphorus (P_{tot}), water colour (colour), primary production (PP), phytoplankton biomass (PB), relative 0–3-year-old perch abundance, and the density of *Chaoborus flavicans* (*Chaoborus*). In addition, the total density of rotifers (Rotatoria, indiv. l^{-1}) was included in the forward selection procedure in the case of crustacean zooplankton. The total densities of cladocerans (Cladocera, indiv. l^{-1}) and cyclopoids (Cyclopoida, indiv. l^{-1}) were included in the forward selection procedure concerning rotifers. In the forward selection procedure, the only variable excluded from both analyses (crustacean zooplankton and rotifers) was *Chaoborus*. A Monte-Carlo permutation test (1000 permutations) was used to test the significance of single variables and RDA axes. As the measurements of variables were related to each other (sampled in successive years from the same lake), the time series option was used as a permutation restriction.

Results

Water quality and other biota

During the study period (1990–2009), monthly-measured alkalinity and pH values increased (SK: 1.6 μeq l^{-1} yr^{-1}, $p < 0.01$; and 0.014 pH unit yr^{-1}, $p < 0.001$; respectively) from 0 μeq l^{-1} and pH ≤ 5 to 30–40 μeq l^{-1} and pH 5.5 (Fig. 1), respectively; and monthly-measured calcium concentration decreased (SK: –0.01 mg l^{-1} yr^{-1}, $p < 0.001$) from ca. 2.5 mg l^{-1} to < 2.0 mg l^{-1}. There was no trend in total phosphorus concentration (mean P_{tot} = 16 μg l^{-1}; SK: $p > 0.1$), but there was an increase in water colour (SK: 2.7 mg l^{-1} yr^{-1}, $p < 0.001$, Fig. 1) and dissolved organic carbon (DOC) concentration (SK: 0.12 mg C l^{-1} yr^{-1}, $p < 0.01$): water colour increased approximately by 50 mg Pt l^{-1} and DOC concentration by 2 mg l^{-1}.

The July water temperature in the surface layer (0–1 m) changed insignificantly from 18 to 19 °C (MK: $Z = 0.811$, $p > 0.1$) whereas in the deeper water layers the temperature significantly decreased (MK: $Z = 2.336$, $p < 0.05$) (Fig. 2). Dissolved oxygen concentration in July decreased clearly, especially at 2 m depth, from 6–8 mg l^{-1} to 0–2 mg l^{-1} (MK: $Z = –4.25$, $p < 0.01$; Fig. 2).

Phytoplankton mean biomass from mid-May to late September varied irregularly from year to year between 1 and 3.5 mg l^{-1}. Primary production, instead, showed a significant decreasing trend (Table 1). The annual mean density of *Chaoborus* larvae was 1–4 indiv. l^{-1} in most years of the 1990s, while a significant decreasing trend during the study period was recorded (*see* Table 1) resulting in densities of 0.1–0.2 indiv. l^{-1} during the last five years.

The strongest year-classes of perch were recorded in the first decade of the study period, but year-to-year variation was high with no clear direction of change (*see* Table 1).

Variability of zooplankton

Between 1990 and 2009 5–10-fold variation in the mean annual densities of the June–August metazoan zooplankton groups was found (Fig. 3). In the years of the highest cladoceran densities, the densities of rotifers appeared to be low. Similarly, during the highest rotifer densities protozoans were scarce.

Altogether 39 rotifer species were identified in the lake. The community was dominated by a few species, of which *Asplanchna priodonta*, *Kellicottia bostoniensis*, *Keratella cochlearis* and *Polyarthra vulgaris* occurred temporarily at densities > 1000 indiv. l^{-1}. None of them showed a significant long-term trend (*see* Table 2). The highest total densities of rotifers, recorded during 1993–1997 (Fig. 3), were mainly due to *K. bostoniensis*, with its greatest mean density

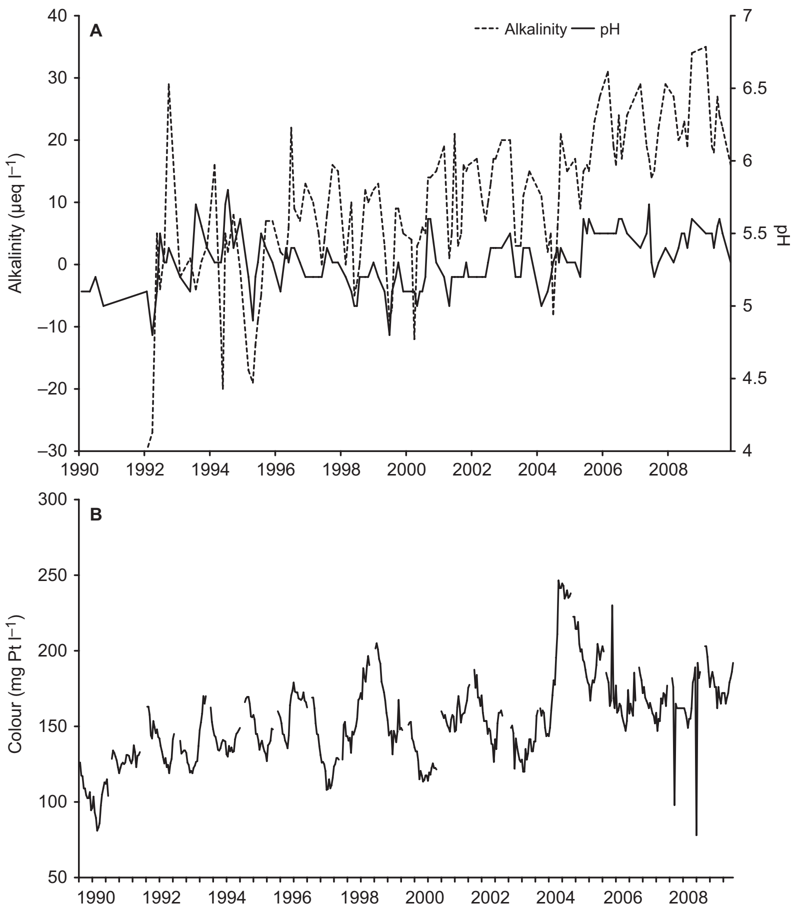

Fig. 1. (**A**) Long-term changes of pH and alkalinity, and (**B**) water colour in lake Valkea-Kotinen during 1990–2009. For more details, *see* Vuorenmaa *et al.* (2014).

(1500 indiv. l^{-1}) in June–August 1995 (Table 2). *Conochiloides coenobasis*, *Keratella hiemalis*, and *Trichocerca similis* occurred temporarily at densities > 100 indiv. l^{-1} (Fig. 4). During the 20-year period, *K. hiemalis*, *K. ticinensis* and *T. similis* showed a significant decreasing trend and *C. coenobasis* an increasing trend (*see* Table 2).

A total of 16 cladoceran species were identified and three of them — *Bosmina longirostris*, *Ceriodaphnia quadrangula* and *Holopedium gibberum* (daily maxima 86, 23 and 108 indiv. l^{-1}, respectively) — together comprised > 93% of the June–August cladoceran mean density (Fig. 4). *Alonella nana*, *Bosmina longispina*, *Chydorus sphaericus*, *Daphnia longispina* and *Diaphanosoma brachyurum* occurred quite regularly but in low densities (< 2 indiv. l^{-1}). Of the dominating species, *B. longirostris* showed a significant increase and *C. quadrangula* a significant decrease (*see* Table 2).

Four copepod species — *Cyclops bohater*, *Cyclops strenuus*, *Mesocyclops leuckarti* and *Thermocyclops oithonoides* occurred regularly in the lake. During the study period, the density of *M. leuckarti* decreased from 30 indiv. l^{-1} to < 5 indiv. l^{-1}. In contrast, the density of *T. oithonoides* increased during the study period and reached 80 indiv. l^{-1} at the highest (Fig. 4). For both species, the trends were significant in August, while in June, July and June–August the trend was significant only for *T. oithonoides* (*see* Table 2). No long term trend was recorded for the *Cyclops* species.

On the basis of the entire 20-year data set, a clear seasonal pattern was recorded for the main taxonomic groups of zooplankton (Fig. 5). The protozoans had their highest densities typically in early June, followed by rotifers in June–July, cladocerans in July and copepods in late July and August.

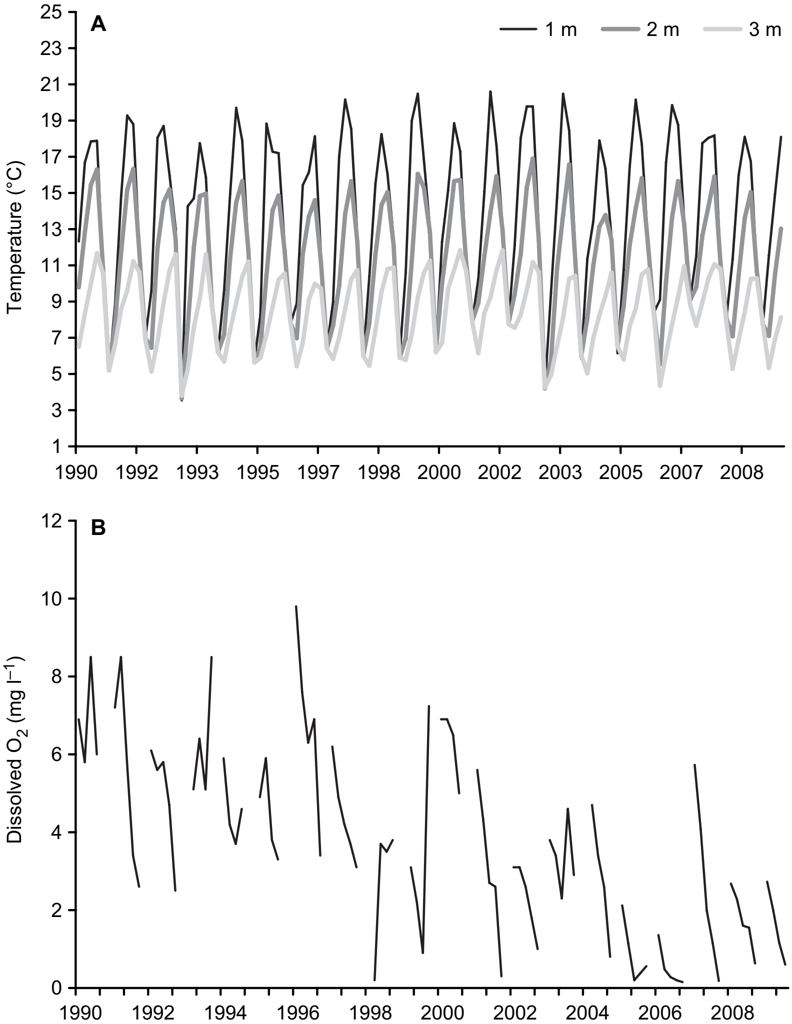

Fig. 2. (**A**) Water temperature in July (at 1 m, 2 m and 3 m), and (**B**) oxygen at 2 m depth in Lake Valkea-Kotinen during 1990–2009.

Among rotifers, almost no changes in the occurrence of highest densities were recorded except for *Kellicottia bostoniensis* and *Polyarthra vulgaris* with a forward shift from June to late July–August for the former and a backward shift from July–August to June for the latter (Fig. 6). The occurrence of maximum density of some crustaceans shifted to slightly later. The most striking shift was found for *Bosmina longirostris* which had its highest densities in June–July in the early years and July–August in the latest years (Fig. 6). The highest densities of *Chaoborus* larvae occurred in August during the 1990s but were recorded in early summer during the latest years (Fig. 6).

Zooplankton responses relative to abiotic and biotic variables

RDA for environmental variables and planktonic rotifer species showed statistically significant relations between the two (Table 3). Of the environmental variables, P_{tot} and temperature had significant effects on the matrix of the rotifers (p = 0.031 and 0.039, respectively). The first RDA axis explained 27% of the variation in the rotifer zooplankton and 42% of the variation in the rotifer zooplankton–environment relations (Table 3). On the first RDA-axis, primary production, P_{tot} and cladoceran density had the highest scores, and alkalinity and water colour

Table 1. Mean phytoplankton biomass, primary production (PP), density of *Chaoborus* larvae and relative year-class strength of perch. The Mann-Kendall test results are also given. For further details of phytoplankton, *see* Arvola *et al*. (2014) and of perch, Rask *et al*. (2014). * = significant at $p < 0.01$.

	Phytoplankton biomass (mg l^{-1})	Primary production (mg C m^{-2} d^{-1})	*Chaoborus* (indiv. l^{-1})	Perch, relative year-class strength
1990	1.8	137	1.3	25
1991	2.6	130	2.1	101
1992	1.2	134	1.6	24
1993	1.5	109	2.1	0
1994	3.2	164	3.8	9
1995	1.6	118	0.6	119
1996	1.7	119	1.1	2
1997	2.4	107	1.6	5
1998	2.4	113	1.7	8
1999	3.4	107	1.8	101
2000	3.6	103	0.6	25
2001	0.9	129	0.8	33
2002	1.4	77	0.5	12
2003	2.8	84	0.2	63
2004	2.3	61	0.3	6
2005	2.5	66	0.1	31
2006	1.6	69	0.2	26
2007	2.1	81	0.1	16
2008	1.8	53	0.2	44
2009	2.6	76	0.1	25
Z	0.552	–4.12*	–3.96*	0.681

Table 2. Seasonal densities (June–August, mean and range) of the most abundant zooplankton species and groups in Lake Valkea-Kotinen during 1990–2009. Mann-Kendall trend analysis results are given for the three summer months and for the average summer abundance. Only significant *Z* values are given ($p < 0.1$ when $|Z| > 1.563$, $p < 0.05$ when $|Z| > 1.862$, $p < 0.01$ when $|Z| > 2.447$).

	Density (indiv. l^{-1})			June	July	August	June–Aug
	Mean	Min	Max				
Cladocera							
Bosmina longirostris	6.3	0.5	25		2.17	4.12	3.34
Ceriodaphnia quadrangula	6.1	0.1	36	–3.54	–3.73	–3.93	–4.19
Holopedium gibberum	4.6	0.9	13				–1.59
Total Cladocera	17	7.8	39				–1.72
Copepoda							
Mesocyclops leuckarti	2.8	0.1	16			–2.50	
Thermocyclops oithonoides	13	0	45	2.30	2.53	2.50	1.91
Adults + copepodites	16	4.7	45				
Nauplii	55	4.6	91				
Rotatoria							
Ascomorpha ecaudis	5.4	0	13				
Asplanchna priodonta	35	3.3	230				
Conochiloides coenobasis	30	0	71	2.76	3.57	3.24	3.67
Kellicottia bostoniensis	317	0	1510				
Keratella cochlearis	158	17	672				
Keratella hiemalis	14	0.7	75	–2.17	–2.89		–2.17
Keratella ticinensis	39	0	176	–3.70	–4.06	–4.19	–3.99
Polyarthra remata	12	0	94				
Polyarthra vulgaris	177	15	849				
Synchaeta spp.	3.4	0	26				
Trichocerca similis	31	0.6	83	–1.59	–1.91		–1.91
Total Rotatoria	833	260	2030				
Protozoa							
Ciliata spp.	26	0	1431				
Total Protozoa	38	0	1442		–2.24	–2.48	–2.03

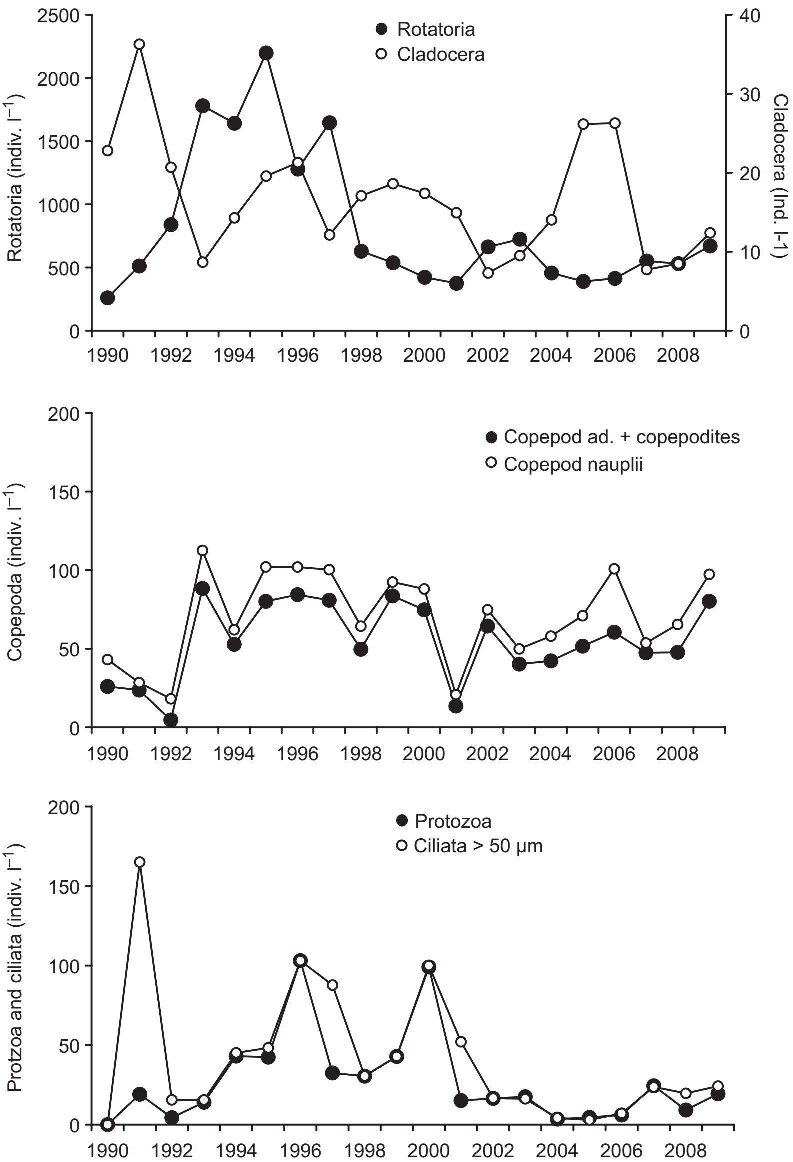

Fig. 3. Mean June–August densities of the main zooplankton groups in Lake Valkea-Kotinen during 1990–2009.

the lowest scores (Fig. 7). Similarly to the RDA for crustacean zooplankton, the first axis indicated environmental gradient, high scores associated with high primary production, nutrients and acidity, and low humic concentration. In addition, cladoceran density had a high score on this axis, which suggests the importance of predation and/or competition on this gradient. Most of the rotifer species had positive scores on the first RDA-axis, especially *K. longispina*, *K. hiemalis*, *K. ticinensis* and *A. priodonta*, while *C. coenobasis* had a high negative score on the axis.

The second RDA-axis explained 18% of the variation in the rotifer variables and 27% of the variation between the rotifer zooplankton and environmental variables (Table 3). High density of copepods, low density of cladocerans, and low temperature characterized this "high competition/predation and cold water" gradient. *Keratella ticinensis*, *T. similis*, *K. bostoniensis* and *K. cochlearis* had high scores and *A. priodonta* a low score on this axis. The last sampling years have scores near zero on this axis indicating that this environmental gradient became less important.

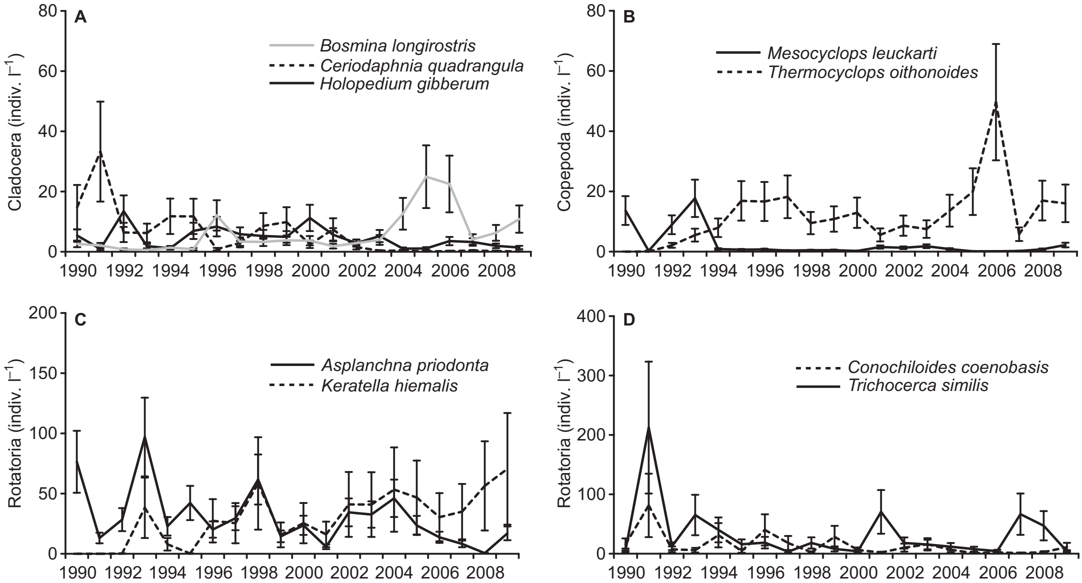

Fig. 4. June–August mean densities (±SD) of the major cladoceran, copepod and rotifer species in Lake Valkea-Kotinen during 1990–2009.

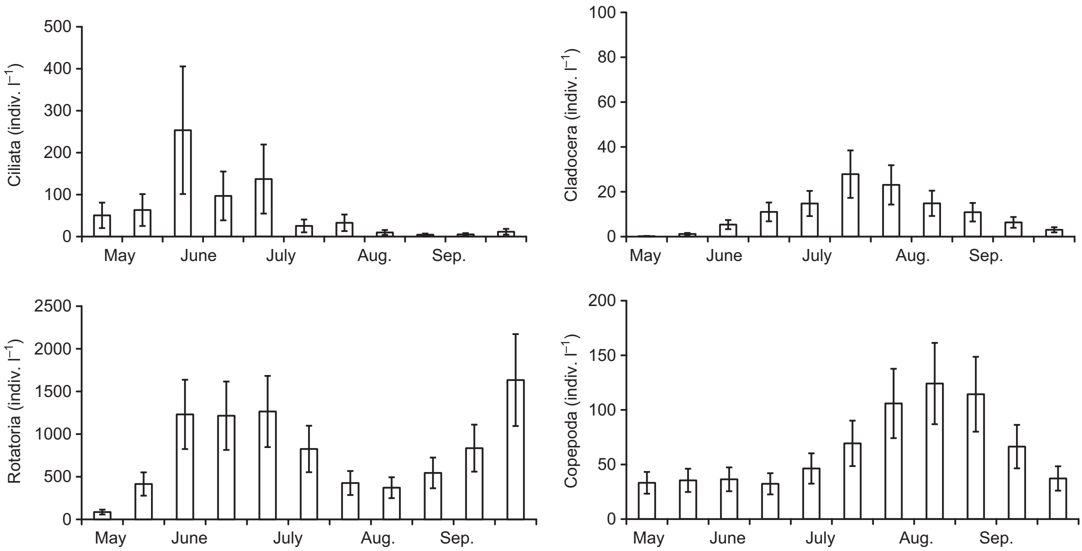

Fig. 5. Seasonal dynamics (mean ± SD) of the major taxonomical groups of zooplankton in 1990–2009 (for rotifers 1996–2003) in Lake Valkea-Kotinen.

In RDA for environmental variables and crustacean zooplankton, the relations between species and environmental variables were statistically significant (*see* Table 4). Of the environmental variables, when considered separately in RDA, water colour, P_{tot} and alkalinity had significant effects on the matrix (p = 0.023, 0.036 and 0.027, respectively). The first RDA-axis, indicating environmental gradient of high primary production, nutrients and acidity, and low water colour (Fig. 8), explained 34% of the variation in the zooplankton and 54% of the variation in the crustacean zooplankton–environment relationship (Table 4). Primary production and total phosphorus had the highest positive scores and water colour and alkalinity the highest negative scores. *Ceriodaphnia quadrangula* and *M. leuckarti* had high positive scores, whereas *T.*

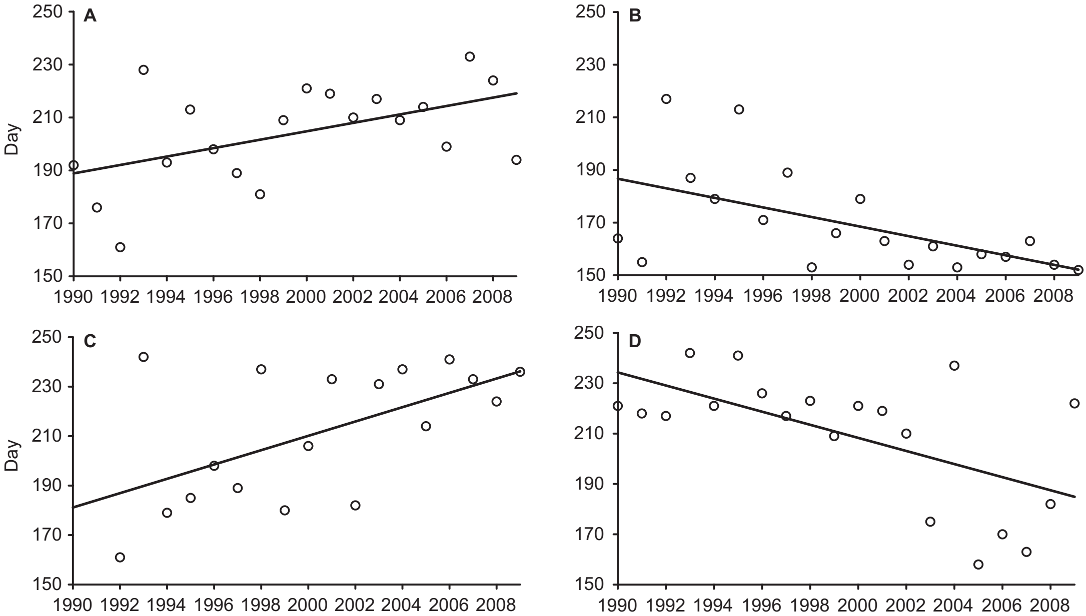

Fig. 6. Examples of seasonal shifts in the occurrence of the highest densities of zooplankton and *Chaoborus* larvae in Lake Valkea-Kotinen during 1990–2009. The lines indicate linear regressions between the study years and the ordinal dates of the highest animal densities. (**A**) *Bosmina longirostris*, (**B**) *Polyarthra vulgaris*, (**C**) *Kellicottia bostoniensis*, and (**D**) *Chaoborus* larvae.

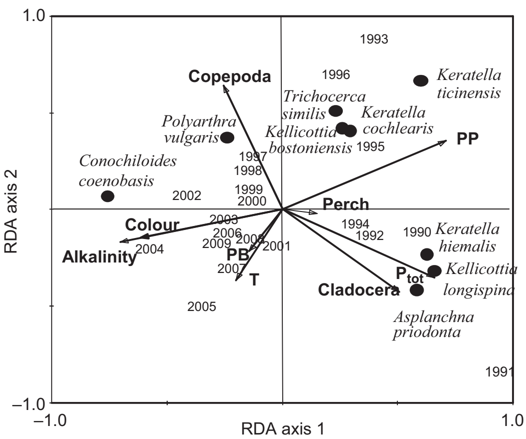

Fig. 7. RDA for biotic and environmental variables (arrows) and the most abundant planktonic rotifer species (filled circles). P_{tot} = total phosphorus, Colour = water colour, T = water temperature, PB = phytoplankton biomass, Perch = relative abundance of 0–3-year-old perch, Rotatoria = density of rotifers, PP = primary production of phytoplankton. Scores for the sampling years are also shown. Eigenvalues (= variance explained of species data × 10^{-2}) can be derived from Table 3.

Table 3. Results of RDA for the most abundant planktonic rotifer species, and biotic and environmental variables during the 20-year monitoring in Lake Valkea-Kotinen.

Variable	Axis 1	Axis 2	All
Rotifer species			
Kellicottia longispina	0.67	–0.33	
Keratella hiemalis	0.64	–0.24	
Keratella ticinensis	0.61	0.67	
Asplanchna priodonta	0.59	–0.42	
Keratella cochlearis	0.30	0.42	
Kellicottia bostoniensis	0.27	0.43	
Trichocerca similis	0.23	0.52	
Polyarthra vulgaris	–0.25	0.38	
Conochiloides coenobasis	–0.77	0.07	
Environmental variables			
Primary production	0.71	0.36	
Total phosphorus	0.66	–0.35	
Cladocera	0.51	–0.43	
Perch abundance (0-3 yr.)	0.15	–0.02	
Phytoplankton biomass	–0.15	–0.22	
Temperature	–0.20	–0.37	
Copepoda	–0.25	0.64	
Water colour	–0.62	–0.15	
Alkalinity	–0.71	–0.17	
F	3.703		2.013
p	0.022		0.022
Variance explained (%)			
Species data	27.02	17.54	60.10
Species–environment relation	41.94	27.22	93.29

oithonoides, *B. longirostris* and Cyclopoida nauplius had high negative scores on this axis. The first sampling years had higher scores on the first RDA-axis as compared with the latest years reflecting the environmental changes during the study period.

The second RDA-axis explained 10% of the variation in the crustacean zooplankton community and 17% of the variation between the crustacean zooplankton and environmental variables (Table 4). P_{tot}, alkalinity and water colour had highly positive and rotifers, primary production and perch abundance highly negative scores on this "high nutrients and alkalinity, low production and rotifers" axis. *Holopedium gibberum* and Cyclopoida nauplius had highly negative scores on this axis (Fig. 8). The last sampling years had higher scores on the second RDA-axis as compared with the first years. Especially, the three latest years are on the sector that has low scores in the first and high scores on the second RDA-axis.

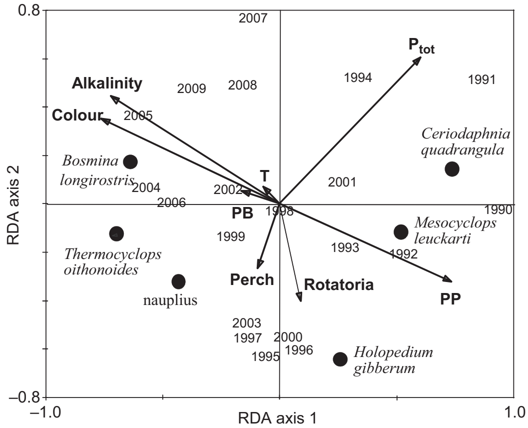

Fig. 8. RDA for biotic and environmental variables (arrows) and the most abundant crustacean zooplankton species (filled circles). P_{tot} = total phosphorus, Colour = water colour, T = water temperature, PB = phytoplankton biomass, Perch = relative abundance of 0–3-year-old perch, Rotatoria = density of rotifers, PP = primary production of phytoplankton. Scores for the sampling years are also shown. Eigenvalues (= variance explained of species data × 10^{-2}) can be derived from Table 4.

Table 4. Results of RDA for the most abundant crustacean zooplankton species, and biotic and environmental variables during the 20-year monitoring in Lake Valkea-Kotinen.

Variable	Axis 1	Axis 2	All
Crustaceans			
Ceriodaphnia quadrangula	0.75	0.15	
Mesocyclops leuckarti	0.54	–0.12	
Holopedium gibberum	0.26	–0.66	
Nauplius	–0.45	–0.33	
Bosmina longirostris	–0.65	0.18	
Thermocyclops oithonoides	–0.71	–0.13	
Environmental variables			
Primary production	0.73	–0.32	
Total phosphorus	0.60	0.61	
Rotatoria	0.09	–0.40	
Temperature	–0.07	0.07	
Perch abundance (0–3-yr-old)	–0.10	–0.27	
Phytoplankton biomass	–0.16	0.05	
Alkalinity	–0.72	0.44	
Water colour	–0.76	0.35	
F	5.678		2.334
p	0.044		0.044
Variance explained (%)			
Species data	34.05	10.49	61.46
Species–environment relation	54.10	16.68	97.68

Discussion

RDA suggested that brownification following the recovery from acidification affected the zooplankton in Lake Valkea-Kotinen strongly. Instead, climate change, if temperature alone is considered, seemed less important, and the same is true for acidity. This is because of the relatively small changes in pH and alkalinity during the study period, and the high tolerance of most of the abundant crustacean and rotifer species to acidity (e.g. Stenson 1973, Arvola *et al*. 1990, Sarvala and Halsinaho 1990, Locke 1991, Hessen *et al*. 1995, Nilssen and Wærvågen 2000). For example, the three most common cladoceran species in Valkea-Kotinen (*Bosmina longirostris*, *Ceriodaphnia quadrangula* and *Holopedium gibberum*) as well as many of the abundant rotifer species were shown to survive at pH levels of 3.5 and 4.0 in a field experiment (Arvola *et al*. 1986), and to make up the major part of the cladoceran and rotifer community in a highly acidic (pH < 4.5) humic lake (Rask *et al*. 1986). Among the dominating cyclopoids in Lake Valkea-Kotinen, *Mesocyclops leuckarti* is known to survive in pH of 4.2 to 4.5 (Jørgensen 1972) and also *Thermocyclops oithonoides* endures pH values < 5.0 (Stenson (1973).

Increasing organic carbon and the subsequent increase in water colour affect aquatic ecosystems in many direct and indirect ways, for example, by contributing to thermal and oxygen stratification, by making the layer of phytoplankton primary production thinner (Arvola *et al*. 2014), affecting the light conditions for visually feeding predators (Estlander *et al*. 2012), and contributing to the energy and carbon sources and processes within the food webs (Salonen *et al*. 1992). In the present study, increasing water colour and humic matter concentrations were associated with the increase of *B. longirostris* and *T. oithonoides* and the decrease of *C. quadrangula* and *M. leuckarti*. These findings are consistent with a paleoecological survey of 49 lakes in Canada, where maximum lake depth and dissolved organic carbon concentration also best explained the structure of the cladoceran assemblages (Korosi and Smol 2011).

Intense water colour may benefit zooplankton by reducing the feeding efficiency of perch, which is a visual feeder and the only planktivorous fish in Lake Valkea-Kotinen (Rask *et al*. 1998, 2014; *see* also Persson *et al*. 1988, Bergman 1988, Estlander *et al*. 2009, 2012), and may explain the minor influence of perch on the zooplankton community, although zooplankton generally contributes significantly to the diet of small perch in small humic lakes (Estlander *et al*. 2012). Nilssen and Wærvågen (2000) suggested that *T. oithonoides* tolerates fish predation better than *M. leuckarti* which is probably because of its smaller size and less coloured body in comparison with *M. leuckarti* (*see* also Viljanen 1983). Our findings are in agreement with those of Nilssen and Wærvågen's because the densities of *M. leuckarti* in Lake Valkea-Kotinen were low during the time of the most abundant cohorts of perch (Rask *et al*. 2014).

Chaoborus larvae which are potentially important predators of pelagic zooplankton (e.g., von Ende and Dempsey 1981) had rather low population density (1.6–3.8 indiv. l^{-1}) but may have played a role in controlling the maximum abundance of the crustacean community. The low density of *Chaborus* in Lake Valkea-Kotinen could have been explained by predation by perch (Rask *et al*. 1998, *see* also Smith and Cooper 1982, Havens 1991), however no relationship between the yearly averages of *Chaoborus* and perch abundance was found in the present study. In a clear water lake nearby, a collapse of the perch population caused an increase of *Chaoborus* larvae (up to 6 indiv. l^{-1}) followed by a drastic drop in the density of pelagic cladocerans (Rask *et al*. 1996).

In Lake Valkea-Kotinen, macrophytes are not very numerous and therefore do not provide protection from fish (Estlander *et al*. 2009). Despite the small size of the lake, a major proportion of its area can be considered a pelagic zone, where the lower part of the epilimnion with decreased oxygen concentrations and rapidly cooling water may act as an important refuge for zooplankton as has been indicated by Manninen (1997). Therefore, the long-term change in oxygen stratification, decreasing oxygen depth, which sets the lower limit of occurrence for zooplankton, may have affected the zooplankton community, both seasonally and in the long term, and may be one reason why some cold-stenothermic rotifer species (*K. hiemalis, K. ticinensis* and *T. similis*) decreased (*see* Berzins & Pejler 1989a, 1989b). However, oxygen was not included in RDA because of its strong correlation with other abiotic variables. The changes in thermal and oxygen stratification, as well as the increasing water colour and patterns in total phosphorus may be attributed, at least partly, to climate change. This emphasizes the indirect importance of climatic factors as drivers of zooplankton dynamics.

In conclusion, in line with the results of Palmer and Yan (2013) the results of this study indicated that crustacean zooplankton was affected by water colour, alkalinity and total phosphorus while rotifers were also affected by both cladocerans and copepods, suggesting competitive and/or predatory interactions. In the early 1990s, the zooplankton community as a whole was closely associated with total phosphorus and primary production of phytoplankton but during the latest years of the study period with water colour and alkalinity. Among the biological variables, primary production of phytoplankton was the most important factor suggesting that the zooplankton community in Lake Valkea-Kotinen was subjected more to bottom-up than to top-down control.

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