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Physical and chemical dynamics of temporary ponds on a calcareous plateau in Thuringia, Germany

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Abstract

Temporary ponds on calcareous hills surrounding the town of Jena (Thuringia, Germany) were investigated for one year with regard to the dynamics of their physical and chemical characteristics. The present paper concerns selected data from a vertical, diurnal and seasonal sampling program including the major physical and chemical factors. The ponds were also investigated during the dry period in summer, and in winter when they are covered with ice. A description of the emergent vegetation is also given and used for a classification of the ponds. Most of the factors investigated show strong diurnal and seasonal trends and some, – despite all ponds being shallow – were vertically stratified. The measurements emphasize that in small ponds both seasonal and diurnal changes in water-chemistry, as well as changes in vertical gradients, are affected by the vegetation succession stage, and consequently by the temporary character of the ponds. Protection and management of these ponds often involves dredging and therefore the short time response of dredging is discussed.

Key words: Temporary ponds – vegetation succession – vertical stratification – dredging

Introduction

Temporary water bodies are those with a recurrent dry period of varying length that is sometimes predictable in its onset and duration (WILLIAMS 1997). The temporary ponds here are "intermittent waters" [under the COMIN & WILLIAMS (1994) classification adopted here] that have a recognizably cyclical pattern of flooding, or became dry at times of the year that are more or less predictable. The seasonal variations of the water level and the drying up cycle are the result of evaporation, seepage, precipitation and ice formation. In temperate regions, a phase of "physiological dryness" can occur in winter when all the water in a pond is frozen.

Temporary ponds are found throughout the world and, although there are considerable regional differences in their type and method of formation, many physical, chemical and biological properties are very similar. The high variability of abiotic factors, and the often comparably variable composition of the fauna, appear particularly important. The world-wide distribution of this water body type leads to a large variety of temporary pond types due to climatic and geological differences. Fluctuations of many physical and chemical factors, are caused by the small size and the drying cycle of temporary waters in the temperate latitudes. The dry period causes faster decomposition of detritus in comparison with permanent waters (NILSSON 1984). This leads to increased food quality of the detritus and to a release of plant nutrients that contribute to the maintenance of high production in temporary waters (WIGGINS et al. 1980). Different rates of vegetation development were caused

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by differences in pond size, pond morphology (proportion of dry area), rate of drying (drying degree), timing of drying, duration of dry period and predictability (reliability of filling) and this leads to long-term persistence of early stages of vegetation succession.

The limnology of temporary waters is poorly documented in comparison to that of larger aquatic ecosystems despite their general ecological interest and ubiquitous distribution (BONNER et al. 1997). WILLIAMS (1985) pointed out that in spite of their relative ubiquity, little is known about the functional dynamics of these systems and knowledge of the winter period is especially poor. Numerous workers have examined changes in some physical and chemical factors, but few studies report the seasonal, diurnal and vertical fluctuations of these factors.

The present study was part of a comprehensive investigation of temporary ponds near the town of Jena (Thuringia, Germany), but this paper deals in particular with the seasonal and diurnal dynamics of different physical and chemical factors. The aim of the study was to identify and quantify variations in oxygen, conductivity, temperature and pH in ponds of different size and stage of vegetation succession. For this purpose, the emergent vegetation was studied and used to produce a classification of the ponds. Particular importance was laid on the question of whether stratifications in the ponds were influenced by pond size and vegetation development. The results are discussed in comparison with other studies of temporary ponds in different regions of the world.

Study site

- General information

The ponds investigated are located on the "Windknollen", a calcareous plateau above the River Saale valley (~360 m a.s.l) between the town of Jena and the village of Cospeda (Thuringia, Germany). The area is very exposed to the wind and the ponds are only little shaded by sparse bank vegetation (see Fig. 1).

This area has a long military history. In 1806 the well-known battle between the armed forces of Napoleon Bonaparte and the armies of Saxony and Prussia took place there, but the area was also used for military exercises in the 20th century. The tanks and other armour-plated heavy vehicles left deep tracks and hollows and, at the end of the 2nd World War, craters were formed by bombs. All these hollows have since filled with water by precipitation (average annual precipitation is 550–650 mm).

All military activities ended in 1990 and the area was declared a nature reserve. More than 300 ponds currently exist within an area of about 1.86 km^2. Most of these ponds are temporary according to the definition of WILLIAMS (1987), with a surface area between 1–400 m^2 and a maximum depth of 5–100 cm. In some ponds rare species occur, including some amphibians, Coleoptera and Odonata. To maintain the biotopes as a refuge, the nature reserve authorities dredge some of the ponds once a year.

Fig. 1. Spring aspect of pond No. 5 (maximum water level; February 1999).

Table 1. Minimum, maximum, means (± 1 standard deviation) of surface area, pond volume and depth of the six ponds investigated. n. m. = not measured.

	Parameter	Pond 1	Pond 2	Pond 3	Pond 4	Pond 5	Pond 6
Before dredging	Surface area (m²)	0.0–21.3 8.63 ± 7.34	0.0–23.2 9.68 ± 7.57	0.0–200 89.1 ± 83.5	0.0–22.9 8.6 ± 9,05	0.0–172.7 83.4 ± 72.6	n. m.
	Volume (m³)	0.0–1.8 0.69 ± 0.65	0.0–1.82 0.66 ± 0.59	0.0–40 15.2 ± 16.2	0.0–2.77 0.94 ± 1.07	0.0–49.6 18.4 ± 19.2	n. m.
	Max. depth (cm)	0.0–24.0 12.7 ± 9.41	0.0–28.4 16.8 ± 10.1	0.0–68.0 37.8 ± 25.1	0.0–43.8 22.2 ± 17.7	0.0–59.7 29.0 ± 23.2	n. m.
After dredging	Surface area (m²)	0.0–21.3 12.4 ± 7.44	0.0–25.3 15.9 ± 7.44	166–383 347 ± 57.2	0.0–31.64 19.5 ± 12.1	20.7–197 141.6 ± 21	63.2–172 136 ± 32.8
	Volume (m³)	0.0–1.8 1.02 ± 0.71	0.0–2.04 1.17 ± 0,65	19.7–98.7 75 ± 23.5	0.0–5.0 2.62 ± 1.9	1.0–46.1 27.1 ± 16.7	5,83–41.4 26.3 ± 11.6
	Max. depth (cm)	0.0–24.0 17.1 ± 7.89	0.0–29.3 23.4 ± 6,72	47.0–76.0 68.0 ± 8.0	0.0–54.5 39.1 ± 15.2	11.4–54.9 38.9 ± 14	31.0–61.0 50.0 ± 9.2

- Ponds investigated

At the beginning of the study program in June 1998, five ponds within an area of less than 2 ha were selected according to the following criteria:

- spatial proximity within a relatively homogeneously structured area;
- a range of different pond sizes (three ponds < 25m² (1, 2 and 4) and two ponds >150 m² (3 and 5);
- different vegetation development (see: classification of the ponds by their vegetation).

Due to the dredging of ponds 3 and 5 in February 1999, another pond >150 m² was included in the investigation (pond 6). The size and depth of the ponds are given in Table 1.

Material and Methods

- Sampling program

The ponds were investigated weekly from June 1998 (pond 6 from February 1999) to August 1999 and maximum depth, air temperature and water temperature, oxygen content, conductivity, and pH were measured at the deepest point. The area around this location was kept free by vegetation during the investigation. Maps of the ponds were used to construct hypsographic curves (polynomial functions) relating pond depth to area and volume.

Oxygen content, conductivity and pH value were measured five centimeters below the surface using portable gages (WTW GmbH, Weilheim, Germany). The measurements were made between 10.00 and 14.00 and, in order to minimize the influence of time of day, the ponds were examined in a different order on each sampling date. Diurnal variations were investigated by taking three-hourly-samples on one day in winter 1998 and two-hourly-samples on one day in spring 1999. The gradients with depth of physical-chemical factors were investigated at different dates by direct fixing of the electrodes at different depths; the first cycle of measurement was made in steps of 2–10 cm from the water surface to a few centimeters above the bottom; the following cycle of measurement was done in the reverse sequence, from the bottom to the water surface. The air temperature was measured with a calibrated thermometer at soil level in a shaded position, immediately after determining of the water temperature.

Further factors investigated were:

Ice cover: In winter ice thickness was measured at the marker over the deepest point. An opening was made in the surface ice as carefully as possible, either with the help of a hand saw or, if the ice cover was thicker, with hammer and chisel. To examine the effects of cryogenic salting out as described by DABORN & CLIFFORD (1974), ice samples were taken and melted in the laboratory at a temperature of 50 °C in a drying furnace. The conductivity of the melt water was determined subsequently.

Dry periods: During dry periods, soil samples were taken in the ponds from within 30 cm of the deepest place and from the surrounding area (one meter from the banks) for the determination of residual moisture. Soil samples were taken with the help of a metal corer (∅ = 5 cm; height = 10 cm). In the laboratory, the fresh mass of the samples and, after drying in a drying furnace (105 °C, 24 h), the dry mass was determined. The residual moisture was used for identifying the dry period since it indicates the drying-degree. The dry soil samples were rewetted (4 ml distilled water per 1 g soil mass), stirred, and filtered after 24 h. The conductivity of the filtrate was then determined.

- Statistics

Statistical analyses were done with the software package SPSS for windows and Sigma Stat 2.0. Normal distribution of data was checked by conducting Kolmogorov-Smirnov-tests.

Seasonal means of the measured factors and mean width of vertical gradients were compared by parametric tests [paired t-test or One Way Analysis of Variance (ANOVA) followed by Tukeys`s HSD tests]. When no normal distribution detected, the raw data were $\log_{10}(x+1)$ transformed to stabilize variances and then checked again by Kolmogorov-Smirnov tests. If this transformation failed to normalize the data distributions, nonparametric tests (Mann-Whitney rank sum test or Kruskal-Wallis analysis of variance on ranks) were used for comparison among medians. To test for correlation's between variations in conductivity and in pond volume linear regression analyses was used.

Results

1. Classification of the ponds by their vegetation

One aim of the study was to characterize the stage of a typical vegetation succession of the ponds and, for this purpose, emergent vegetation is an important criterion. Other factors were the coverage of the bottom with rotting vegetable material, the anaerobic sludge formation, and the silting-up tendencies (these factors were not measured, but only observed). For the six ponds investigated these characteristics are given in Table 2.

In the classification of the emergent vegetation [modified after Stewart & Kantrud (1971)], three different grades are used:

I – fragmented marginal bands;
II – continuos marginal bands;
III – closed stands of emergents covering more than 80% and the area of open water or bare soil comprising less than 20% of the wetland area.

A further criterion were the "vegetation units" based on the zonation of vegetation on the banks and the littoral. For the ponds of the "Windknollen" studied in 1998/1999, a pattern of six different vegetation units was characteristic (see also Table 2):

(1) The *Deschampsia*-zone, named after *Deschampsia caespitosa* (L.) P.B., which together with other plants such as *Festuca rubra* (L.), *Epilobium palustre* (L.) and *Ophioglossum vulgatum* (L.) forms a zone nearby or around the pond.

(2) *Deschampsia*-zone is followed by the *Juncus*-belt, named after *Juncus inflexus* (L.), *J. articulatus* (C. em. Richter) and *J. bufonius* (L.).

(3) In the shallow open-water zone beyond the *Juncus*-belt occurs a zone with submerged species like *Eleocharis palustris* (C.) R. et Sch. and aquatic mosses

Table 2. Main characteristics for classification of vegetation succession stage in the ponds studied. The classes of emergent vegetation cover used are: (I) fragmented marginal bands, (II) continuos marginal bands and (III) closed stands of emergents covering more than 80% and the area of open water or bare soils comprising less than 20% of the wet-land area. These classes are used to indicate the presence of the different vegetation units: (1) *Deschampsia*-zone, (2) *Juncus inflexus*-belt, (3) *Eleocharis palustris*-zone, (4) *Chara fragilis*-lawn, (5) *Typha latifolia*-stands, (6) arable-weed belt. Further common characteristics of succession stage and pond age classified by three different grades: the character was not found (X), to a small extent (XX), to a medium extent (XXX) or to large extent in the pond (XXXX).

	Pond No.	Vegetation units						Coverage of the bottom (BOM)	Anaerobic sludge formation	Silting-up tendencies
		1	2	3	4	5	6			
Before dredging	4	I						XX	X	X
	1	I	I	II	II	I		XX	XX	XXX
	5	I	I	II	II	I		XX	XX	XXX
	2	I	II	II	I	II		XXX	XXX	XXXX
	3	I	III	III	I	III		XXXX	XXXX	XXXX
After dredging	4	I						XX	X	X
	3	I		I	III	I	II	XX	X	X
	5	I		I	III	I	II	XX	X	X
	1	I	I	II	II	I		XX	XX	XXX
	2	I	II	II	I	II		XXX	XXX	XXXX
	6	I	III	III	I	III		XXXX	XXXX	XXXX

(*Drepanocladus* sp.). Occasional single specimens of *Alisma plantago-aquatica* (L.) and *Alisma lanceolatum* (WITH.) are also typical for this zone.

(4) In the deeper water areas *Chara fragilis* is dominant, mostly within the area of the deepest part of the pond, but dependent upon the stage of succession and the size of the pond.

(5) Stands of *Typha latifolia* (L.) formed a fifth vegetation unit. Typical here are also *Hydrocharis morsus-ranae* (L.) and *Utricularia australis* (R. BR.).

(6) In dredged ponds, the *Juncus*-belt was replaced by another vegetation unit in which the dominating plants are arable-weeds [*Plantago intermedia* (GILIB.), *Kickxia spuria* (L.) DUM. and *Centaurium pulchellum* (SW.) DRUCE].

Table 2 shows that vegetation unit 1 was present in every pond.

The main characteristics of vegetation succession in the ponds investigated were: (a) a progressive increase in coverage by emergent plants and (b) a progressive decrease of vegetation unit 4, accompanied by an increase of vegetation unit 5.

According to this evidence, in the period before dredging, ponds 1 and 5 represent an earlier, and ponds 2 and 3 a higher, maturity stage of a hypothetical vegetation succession (compare Table 2). After dredging ponds 3 and 5, vegetation unit 2 was replaced by an arable-weed belt, vegetation unit 3 was interrupted or disappeared completely, *Chara fragilis* became dominant (extremely), some *Typha latifolia* rhizomes survived the dredging and formed a patch near the deepest place. The vegetation succession pattern in pond 6 was very similar to the pattern observed in pond 3 before it was dredged.

In contrast to the other ponds, pond 4 had no clear pattern of vegetation units, some macrophytes of the six different vegetation units occurred without order (azonal). A typical species in this pond was *Carex otrubae* (PODP.); and besides *Deschampsia caespitosa* (L.) P.B. and *Juncus inflexus* (L.) many grassland species could be found. Pond 4 represents a special type of a succession-stage that can be found frequently in the investigation area. A high proportion of briefly flooded grass areas with sparse aquatic vegetation where bog and aquatic plants are limited to the deeper areas characterizes this type of pond. The morphology of these ponds results in large water level fluctuations and in the distribution of the vegetation described above. This type of pond probably remains in an initial stage of vegetation succession for a considerable extended time.

2. Water level in the different seasons and the drying up cycle

The ponds showed a very similar seasonal cycle in terms of their water level in the course of the year. Fig. 2 shows the changes in water levels for the investigation period. Our investigation started in June 1998, a short time before the ponds dry out. Refilling occurs in September 1998. In the 1998/1999 winter, two periods with thick ice development were observed but none of the ponds

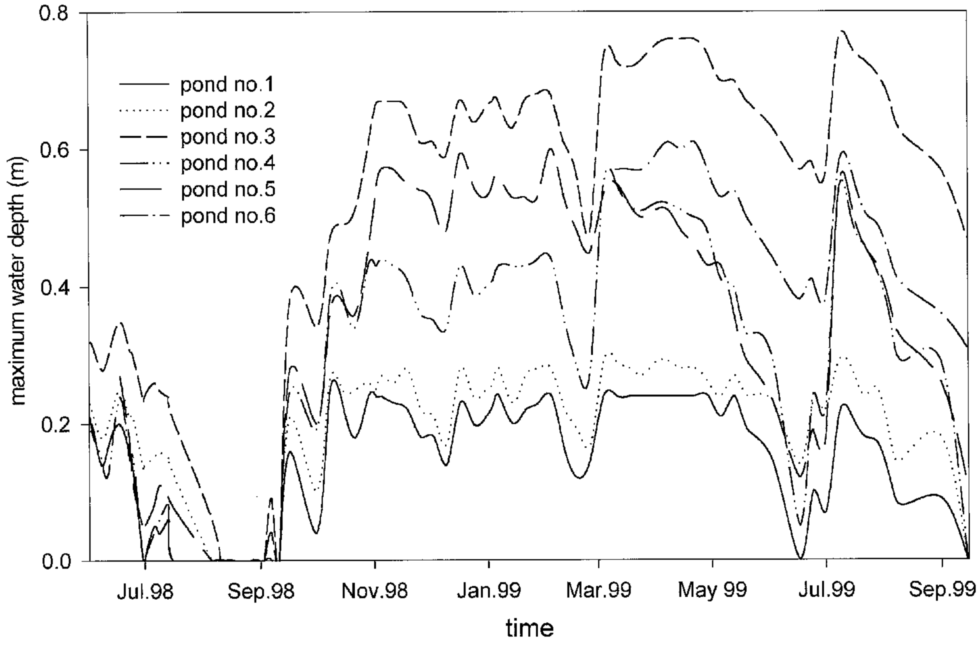

Fig. 2. Seasonal water-level fluctuations in the ponds during the study period.

Table 3. Minimum, maximum, mean (±1 standard deviation) of additional pond characteristics.

Parameter	Pond 1	Pond 2	Pond 3	Pond 4	Pond 5	Bank soil
Drying degree 1998 (residual moisture) (%)	9.3–27.5	29.0–55.0	52.4–82.9	44.0–80.6	17.5–52.7	5.95–30.6
	19.2 ± 4.78	37.1 ± 8.33	70.7 ± 8.63	56.9 ± 10.4	29.8 ± 9.9	18.0 ± 9.0
Conductivity of soil samples (µS cm^{-1})	501–1133	561–1870	2900–6360	698–1680	970–2640	310–464
	731 ± 198	866 ± 369	4378 ± 1292	1107 ± 254	1603 ± 527	357 ± 50.4
Ice cover (cm)	0.2–17.5	0.2–14.4	0.2–14.0	0.2–15.7	0.2–12.7	–
	5.5 ± 5.8	4.7 ± 4.9	3.3 ± 4.0	4.5 ± 5.3	3.1 ± 3.8	–
Frozen volume (%)	5.8–89.3	10.34–87.4	0.45–78.3	4.4–90.9	1.52–38.2	–
	39.4 ± 29.6	46.3 ± 26.1	19.2 ± 20.4	52.9 ± 25.8	19.9 ± 9.2	–
Conductivity of ice samples (µS cm^{-1})	42.8–300	59–248	37.4–266	25.1–219	23.0–140	–
	157.8 ± 83.4	118.6 ± 65.3	142.3 ± 83.3	108.3 ± 67.5	89.9 ± 46.3	–

froze completely from the surface to the bottom. During the period with greatest ice development, up to 90% of the pond volume was frozen (especially in the smaller ponds). In March 1999, after thawing and extensive spring precipitation, all ponds were ice-free, maximally filled, and overflow occurred. After this month the water levels dropped steadily. In June 1999, the water levels reached the same values as in the year before (with exception of pond 3). In July 1998, all ponds were filled by extremely high precipitation up to maximum capacity within a few days, and thus interrupted the drying cycle. The ponds in the surrounding area that were already partially dried out in March/April were also filled again. Table 3 gives an overview of drying degrees that occur in the soils of the ponds during the drying period in 1998 and for further pond characteristics.

3. Physical-chemical characteristics

Periodic filling and drying resulted in strange physical and chemical fluctuations in the ponds.

The mean, maximum and minimum values for conductivity, pH, oxygen content and temperature are given in Table 4.

- **Conductivity**

Seasonal investigations: Strong, almost simultaneous, seasonal variations of conductivity were observed in all six ponds investigated (Fig. 3). The maximum values were measured at the beginning and the end of the dry period (mid June and mid September 1998), coupled with very small water volumes. The mean conductivity in the spring / summer period of 1999 was lower than during the winter (period between first and last ice cover) ($p < 0.05$; Mann-Whitney U-test). Conductivity and variations in volume were correlated (maximum: $R = 0.7433$, $p < 0.001/\alpha = 1$ in pond 1; minimum: $R = 0.2$, $p < 0.001/\alpha = 1$ in pond 3). In the refilling period there was a strong negative connection between volume and conductivity.

In 70% of all cases, an increase of pond volume was coupled with a decrease of conductivity, and vice versa. In the period before dredging no differences could be found between the mean conductivity values in surface layers of the ponds ($p > 0.001$; ANOVA, post hoc: Tukey's HSD test). After dredging, surface layer conductivity in pond 3 and 5 was reduced in comparison to the values in the undisturbed ponds ($p < 0.01$; ANOVA, post hoc: Tukey's HSD test).

In winter, the conductivity in the ponds was strongly influenced by cryogenic salting out (DABORN & CLIFFORD 1974). In pond 1, for instance, conductivity increased threefold in the residual water under the ice cover during the first period of strong ice development (December 1998). The conductivity of the melted ice samples had a mean of 123 µS cm^{-1}, clearly smaller than the conductivity of the water under the ice cover ($p < 0.05$; Mann-Whitney-U test) and smaller than the minimum values measured during the whole season.

Vertical and diurnal investigations: In most of the vertical measurements made, a clear vertical stratification of conductivity occurred and some stratifications are shown in Fig. 4. The values of the surface layers were generally smaller than those of the bottom layers. The maximum, minimum and mean width of gradients are listed in Table 5. The maximum measured gradient occurred in pond 3 on February 4, 1999 (5 cm water-depth: 410 µS cm^{-1}, ~65 cm depth: 2560 µS cm^{-1}). In dredged ponds the stratification of conductivity was reduced in the spring (see Table 6). However, in the other, non-dredged, ponds, gradients were also lower in spring and summer in comparison to those in winter ($p < 0.05$; ANOVA, post hoc: Tukey's HSD test). In diurnal measurements in winter 1998 and spring 1999 no clear daily cycle could be found.

Table 4. Mean (±1 standard deviation), maximum and minimum conductivity values, pH values, oxygen content, water temperature (surface measurement – 5 cm depth) in the ponds during the study period. n. m. = not measured.

	Parameter	Pond 1	Pond 2	Pond 3	Pond 4	Pond 5	Pond 6
Before dredging	Conductivity (µS cm^{-1})	401–2040 871 ± 431	476–1001 735 ± 147	394–2700 856 ± 440	423–1587 691 ± 267	430–2720 696 ± 472	n. m.
	pH	7.13–8.51 7.81 ± 0.42	7.13–8.60 7.72 ± 0.27	7.28–8.66 7.77 ± 0,29	7.32–8.17 7.70 ± 0.24	7.36–8.66 8.11 ± 0.37	n. m.
	Oxygen saturation (%)	17–192 92.8 ± 40.9	12–156 72.8 ± 37.7	1–150 70.4 ± 36.0	9–123 55.9 ± 30.2	4–190 91.7 ± 45.9	n. m.
	Oxygen content (mg l^{-1})	1.3–26.3 10.7 ± 5.7	1.1–20.3 8.6 ± 5.0	0.1–18.0 8.1 ± 4.3	1.0–15.1 6.3 ± 3.5	0.3–24.3 10.8 ± 5.9	n. m.
	Temperature (°C)	0.0–28.1 8.55 ± 8.29	0.1–24.8 7.93 ± 7.63	0.0–27.7 9.16 ± 8.51	0.0–25.2 8.28 ± 7.78	0.1–25.1 8.23 ± 8.32	n. m.
After dredging	Conductivity (µS cm^{-1})	400–1459 722 ± 226	397–704 603 ± 70.8	295–730 529 ± 146	310–1135 582 ± 181	294–689 440 ± 99.4	339–592 478 ± 81.0
	pH	7.02–8.50 7.88 ± 0.45	7.03–8.08 7.56 ± 0.26	8.25–9.62 8.67 ± 0,44	7.28–8.33 7.87 ± 0.24	7.90–8.67 8.37 ± 0.18	7.42–8.62 7,91 ± 0.34
	Oxygen saturation (%)	17–181 104 ± 42.5	33–87 61.2 ± 17.5	71–144 97.9 ± 19.8	34–139 76.5 ± 23.6	56–172 104 ± 22.6	46–147 89.7 ± 25.7
	Oxygen content (mg l^{-1})	1.4–18.0 9.3 ± 4.5	2.8–10.3 5.7 ± 2.1	6.4–11.9 9.2 ± 1.4	3.0–11.2 6.9 ± 2.0	4.6–13.4 9.4 ± 2.0	4.2–12.7 8.7 ± 2.4
	Temperature (°C)	5.2–26.1 17.5 ± 6.20	3.5–23.8 15.3 ± 6.27	3.5–26.6 16.0 ± 6.87	4.8–26.1 17.2 ± 6.27	4.0–27.5 17.8 ± 7.23	4.2–24.5 15.2 ± 6.34

- **pH-value**

Seasonal investigations: Water was generally alkaline in the ponds and clear seasonal trends occurred (Fig. 3).

In June 1998, the pH value in all six ponds decreased with decreasing water levels. During the refilling period (1998) and in spring (1999) pH > 8 were measured in all ponds. In summer 1999 pH gradually decreased in the undisturbed ponds towards the end of the hydrological cycle. In the two dredged ponds (3 and 5) pH also decreased until July 1999, but after heavy rainstorms and pond refilling, pH increased to values higher than pH 8.5. With an increase of the thickness of ice cover in winter (ice thickness also being a surrogate for the length of time the ponds had been frozen) the pH value of the water beneath the ice fell precipitately. In the period before dredging, the pH of the larger ponds (3 and 5) was significant higher in comparison to the smaller ponds ($p < 0.01$, ANOVA, post hoc: Tukey's HSD test) In the dredged ponds, the pH values of the surface layers were significantly higher ($p < 0.001$; ANOVA, post hoc: Tukey's HSD test) than that of the undisturbed ponds.

Vertical and diurnal investigations: In most of the ponds investigated a vertical stratification of the pH values appeared. Fig. 5 gives some examples for winter and summer months. The gradient width seems to be independent of the water depth, and the pH in the surface layers was higher than those of the bottom layers. At the bottom a pH near 7.0 was frequently measured. After ponds 3 and 5 were dredged, pH was unstratified (Table 6). In spring there was a clear diurnal cycle (Fig. 6), with an increase during the daytime and a decrease during night. The largest rise was found in the surface layers (5 cm depth). The vertical pH gradient also remained during the night, although only with smaller amplitude than by day. In winter the pH vertical gradient was stable during the whole day, without larger fluctuations.

- **Oxygen content**

Seasonal investigations: Dissolved oxygen varied between 0.1 mg l^{-1} and 26.3 mg l^{-1}, this corresponds to an oxygen saturation between 1% and 192%. The maximum values were measured in the winter and spring (see Fig. 3). Oxygen saturation decreased with decreasing water levels in summer 1998 and 1999 up to a minimum briefly before dry up. In two strong ice periods in winter, oxygen was also strongly reduced. In the period before dredging, mean oxygen content followed the successional trend (ponds 1 and 5 > ponds 2 and 3 > pond 4) ($p < 0.05$; ANOVA, post hoc: Tukey's HSD test). Dredg-

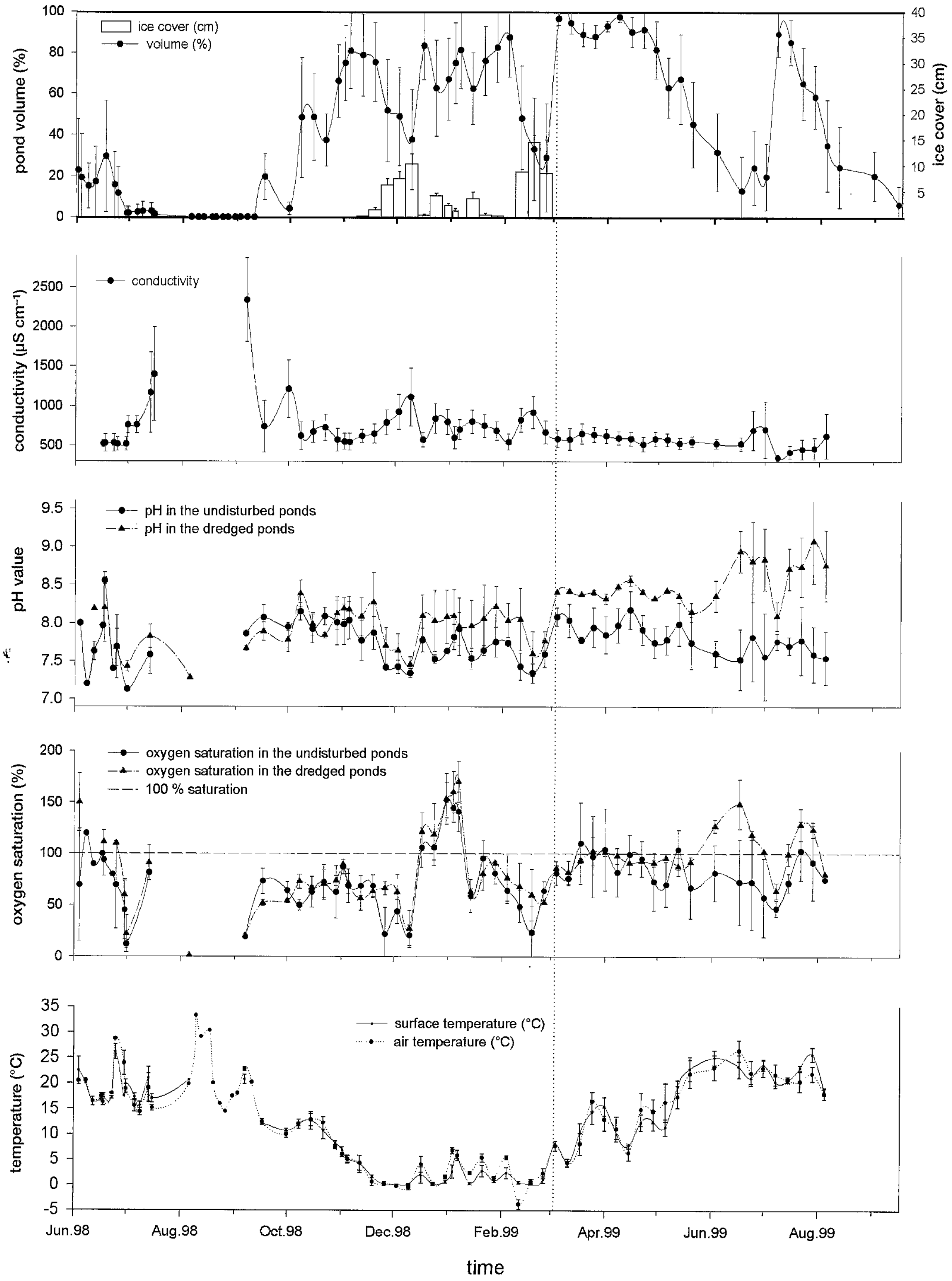
ice cover (cm)
volume (%)
pond volume (%)
ice cover (cm)
100
80
60
40
20
0
40
35
30
25
20
15
10
5
conductivity
conductivity (µS cm⁻¹)
2500
2000
1500
1000
500
pH in the undisturbed ponds
pH in the dredged ponds
pH value
9.5
9.0
8.5
8.0
7.5
7.0
oxygen saturation in the undisturbed ponds
oxygen saturation in the dredged ponds
100 % saturation
oxygen saturation (%)
200
150
100
50
0
surface temperature (°C)
air temperature (°C)
temperature (°C)
35
30
25
20
15
10
5
0
-5
Jun.98
Aug.98
Oct.98
Dec.98
Feb.99
Apr.99
Jun.99
Aug.99
time

Table 5. Mean (± 1 standard deviation), maximum and minimum values of vertical conductivity gradients in the ponds during the study period. Vertical temperature gradients are given as mathematical absolute values. n.m. = not measured.

	Parameter	Pond 1	Pond 2	Pond 3	Pond 4	Pond 5	Pond 6
Before dredging	Conductivity, vertical gradients (µS cm^{-1})	55–1106 359 ± 264	91–620 347 ± 175	820–2144 1471 ± 310	59–476 281 ± 107	116–2040 1443 ± 508	n. m.
	Temperature, vertical gradients (°C)	0.1–3.2 1.39 ± 0.99	0.0–3.2 1.58 ± 0.99	0.7–6.0 4.3 ± 1.31	0.2–4.4 2.47 ± 1.21	0.6–5.1 3.29 ± 1.36	n. m.
After-dredging	Conductivity, vertical gradients (µS cm^{-1})	63–578 222 ± 129	5–748 301 ± 217	0–389 73 ± 100	0–610 146 ± 165	2–306 72 ± 97	8–828 230 ± 172
	Temperature, vertical gradients (°C)	0.0–8.3 3.20 ± 2.54	0.2–6.4 2.70 ± 1.84	0.0–2.9 0.88 ± 0.90	0.8–7.9 3.66 ± 2.49	0.0–7.9 1.48 ± 2.11	0.2–4.2 1.93 ± 1.34

Table 6. Comparison of vertical stratification on the basis of the mean (± 1 standard deviation), maximum and minimum values for several factors in the period after dredging. Vertical temperature and oxygen gradients are given as mathematical absolute values.

Parameter	Undisturbed ponds (Pond 1, 2, 4 & 6)	Dredged ponds (Pond 3 & 5)
Conductivity, vertical gradients (µS cm^{-1})	0.0–828 227 ± 181	0.0–389 73 ± 98
Temperature, vertical gradients (°C)	0.0–8.3 2.86 ± 2.16	0.0–7,9 0.92 ± 0.96
pH, vertical gradients	0.03–1.47 0.54 ± 0.37	–0.01–0.16 0.05 ± 0.05
Oxygen, vertical gradients (%)	1.0–91.0 31.2 ± 19.3	1.0–31 12.6 ± 8.7
Oxygen, vertical gradients (mg l^{-1})	0.0–6.8 2.49 ± 1.77	0.0–2.1 0.99 ± 0.77

ing leads to an increase of oxygen content in comparison to undisturbed ponds ($p < 0.05$; ANOVA, post hoc: Tukey's HSD test) (see Table 6).

Vertical and diurnal investigations: In spring, a clear diurnal cycle was also observed (Fig. 6). In winter periods with thick ice cover, oxygen content was generally low and no diurnal fluctuations were determined. Despite the shallowness of the water vertical stratification of oxygen could be observed in the ponds. The oxygen content in the layers near to the bottom was often lower than that of the surface layers. Only in a few cases the oxygen was evenly distributed or showed inverse gradients. After dredging, oxygen stratification was greatly reduced and oxygen seems to be more evenly distributed ($p < 0.05$; ANOVA, post hoc: Tukey's HSD test) (see Table 6). Fig. 7 shows some vertical oxygen stratifications.

- **Temperature**

Seasonal measurements: The water-temperature is strongly dependent on the air and ground temperature and follows the typical annual temperature cycle of temperate regions. Fig. 3 shows the temperature cycle during the investigation. Despite the different volumes of the ponds, there was no difference between annual mean surface temperatures ($p < 0.05$; ANOVA, post hoc: Tukey's HSD test).

Fig. 3. Seasonal dynamics of several physical and chemical factors for the study ponds on basis of surface measurements (5 cm depth). Mean values for the factors, error bars represent standard deviation. The pond volume is given in percent (0% – dry; 100% – maximal filled and overflow occurs). The vertical dotted line marks the date of dredging (pond no. 3 and no. 5).

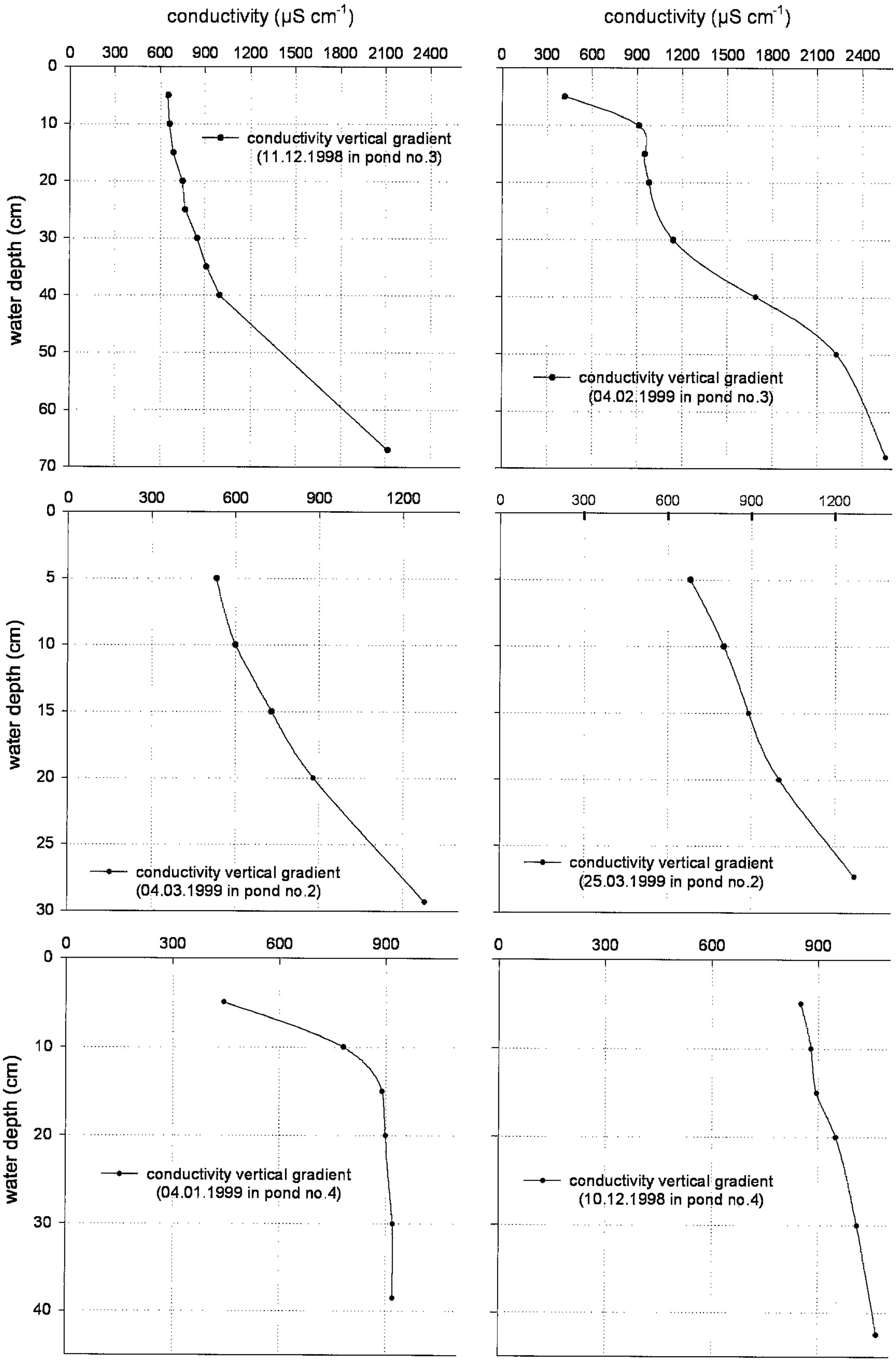

Fig. 4. Some examples for vertical conductivity gradients.

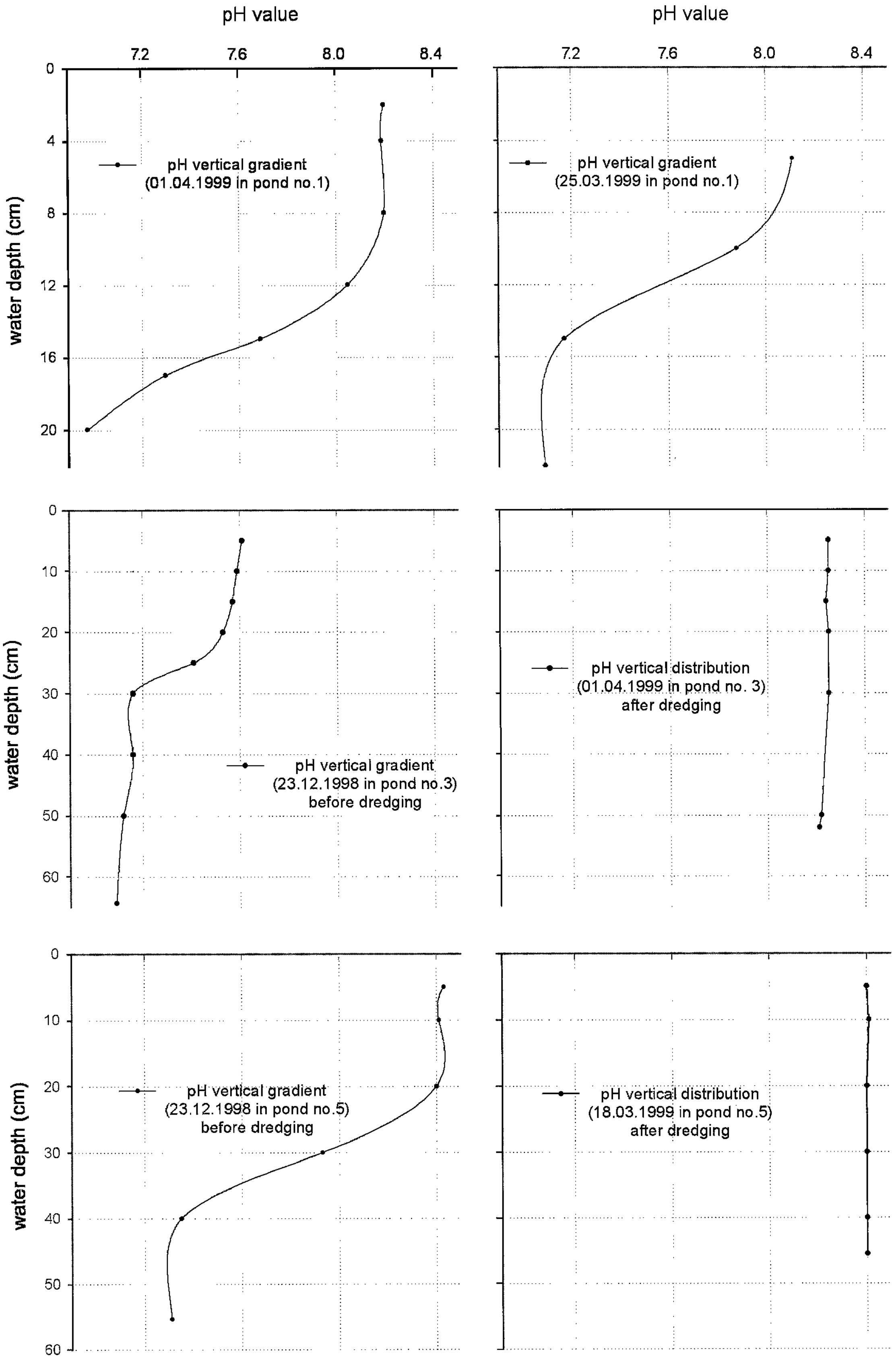

Fig. 5. Some examples for vertical pH gradients.

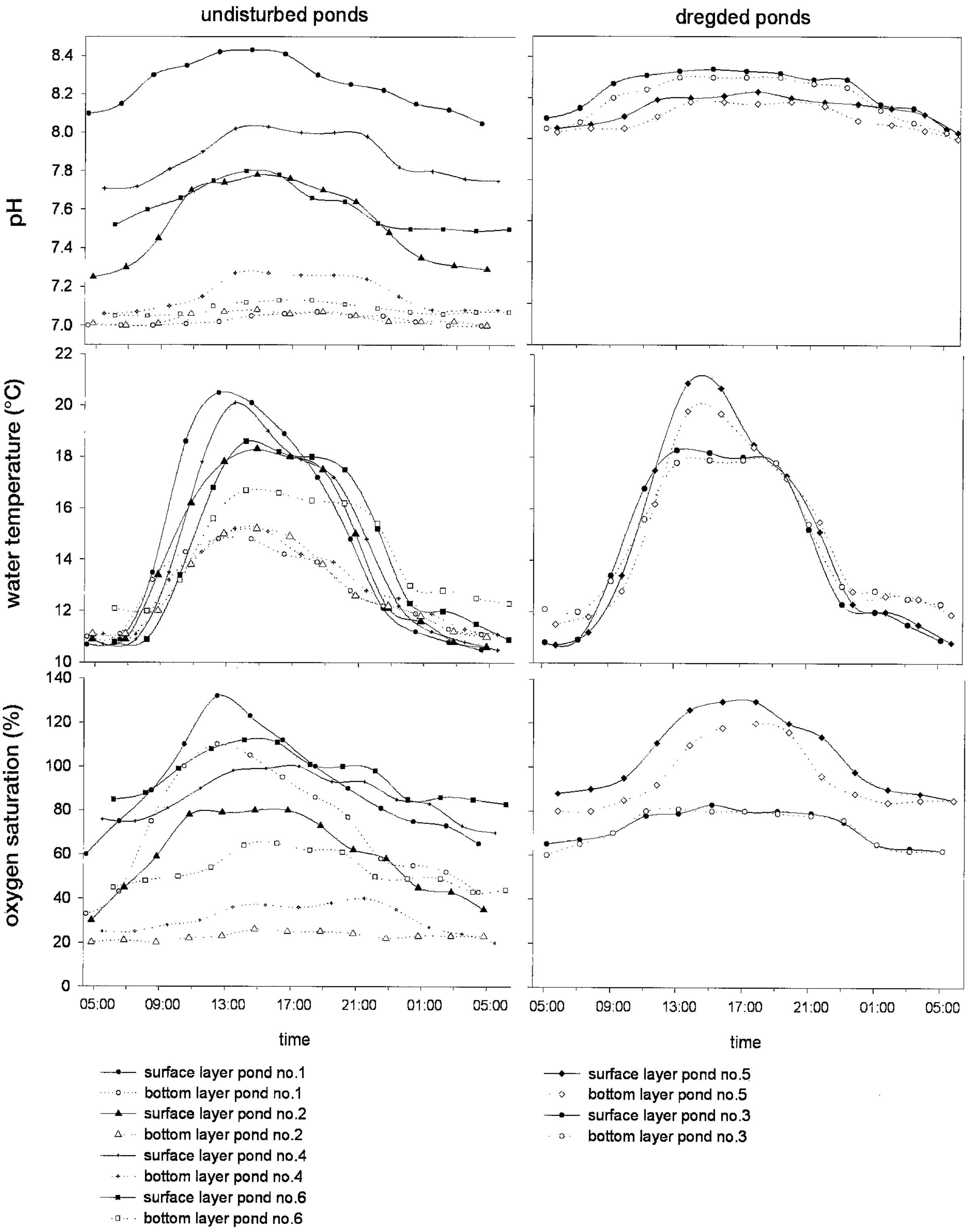

Fig. 6. Diurnal cycles for pH, oxygen and temperature in spring. Undisturbed ponds on the graphs left, dredged ponds on the graphs right. Solid lines mark surface layers (5 cm depth); dotted lines mark bottom layers.

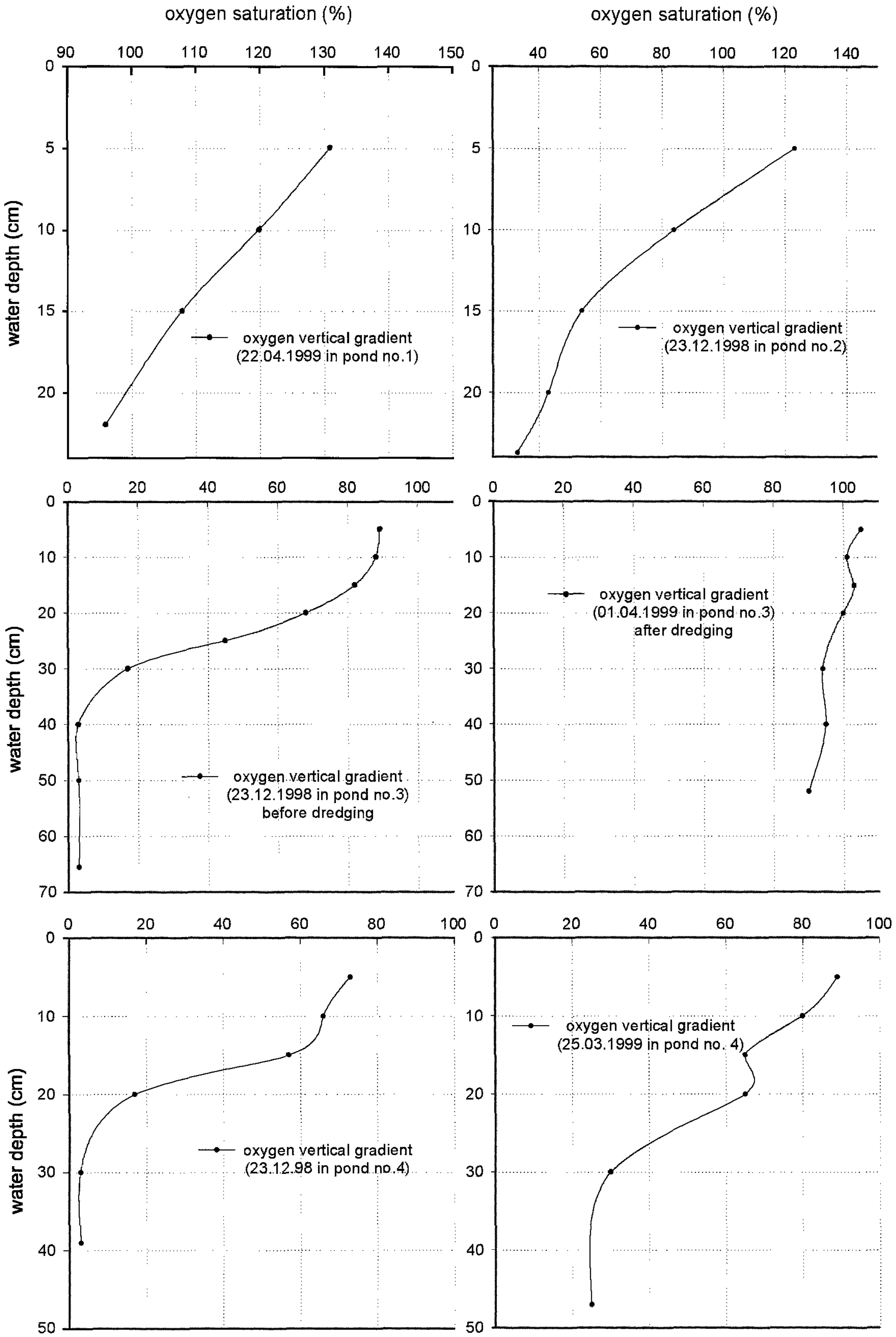

Fig. 7. Some examples for vertical oxygen gradients.

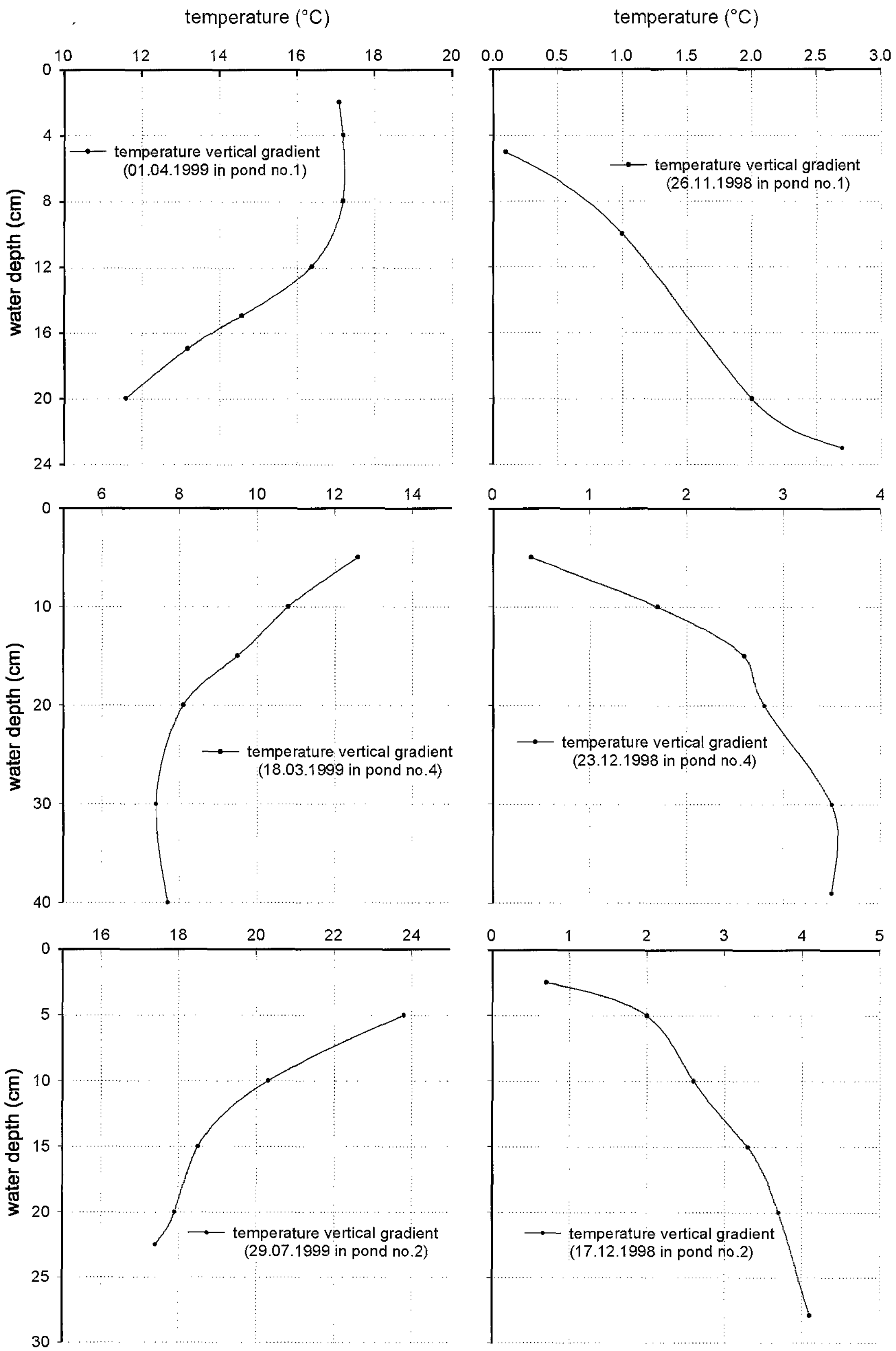

Fig. 8. Some examples for vertical temperature gradients.

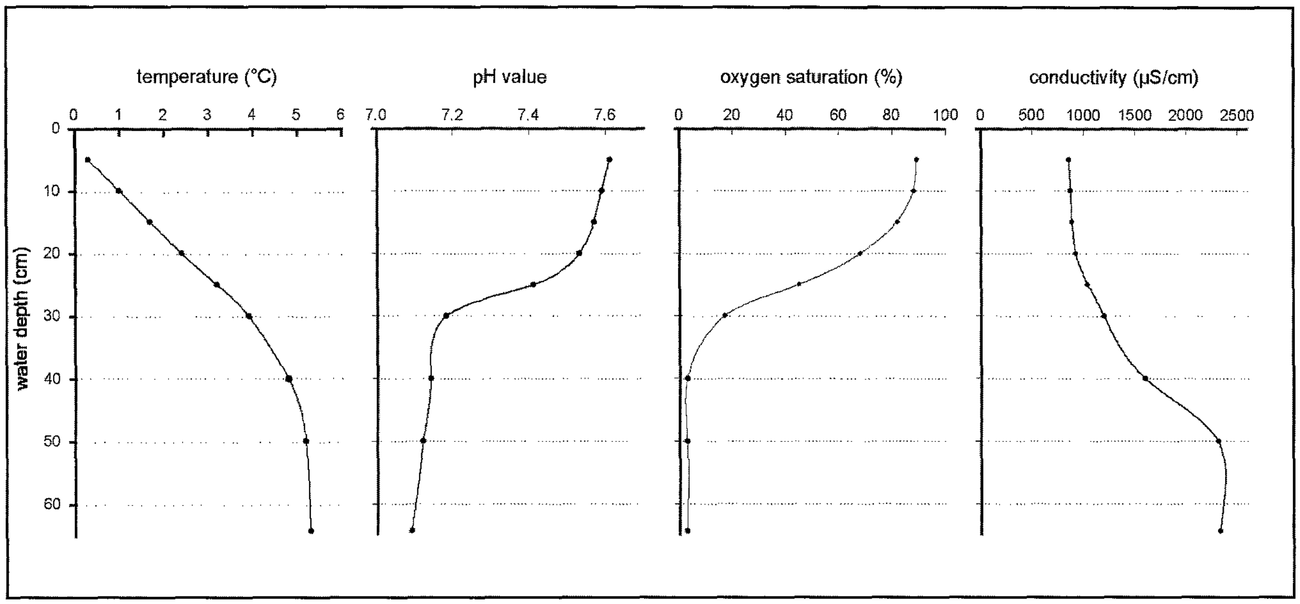

Fig. 9. Typical vertical stratification of temperature, pH value, oxygen and conductivity during winter periods with strong ice cover in the larger ponds (ponds no. 3 and 5).

Vertical and diurnal investigations: Often direct or inverse vertical gradients of temperature could be determined (Fig. 8) The maximum temperature difference between surface and bottom (8.3 °C) was measured in the smallest pond (pond 1, max. depth 18.5 cm) on 20.05.1999. The mean, maximum and minimum values of the temperature gradients are listed in Table 5. In winter before dredging, the larger ponds (3 and 5) showed steeper thermal gradients in comparison to the smaller ponds ($p < 0.01$; ANOVA, post hoc: Tukey's HSD test). In the two dredged ponds, the mean difference between surface and bottom layers was lower in comparison to those in the undisturbed ponds ($p < 0.05$, paired t-test) (see Table 6). In both dredged ponds, a non-periodic homothermy, or small direct temperature stratification, was common. In winter periods with ice cover, inverse temperature gradients were usually measured (Fig. 8). The maximum difference of the inverse gradients lay between 3.2 to 7.6 °C. Diurnal temperature measurements in spring resulted in a clear cycle (see Fig. 6). Direct stratification occurs during day. At night, an inverse temperature gradient was formed. Diurnal measurements in winter did not result in clear changes of the indirect temperature gradients in the course of the day.

In the larger ponds (3 and 5), in the winter a very interesting pattern was observed. The width of the inverse temperature gradient ranged often up to 7 °C. At the depth with a temperature of 4 °C remarkable changes of pH and oxygen gradients occur since both of them decrease strongly (see Fig. 9).

Discussion

All the physical and chemical features investigated fluctuate seasonally and diurnally between wide ranges. Precipitation represents the main source of water for the ponds of the study site and water losses arose from evaporation and seepage. Water is also certainly lost through transpiration by plants. The extremely dry soils between ponds indicate that little water is lost or gained through seepage through the soil. This is probably because of the very impervious nature of the local clay substrata.

Wiggins et al. (1980) pointed out that temporary waters can change their character in years with greatly different amounts of precipitation regarding the temporary cycle (see this investigation). Physiological dryness in winter is a common feature of small ponds in temperate and cold regions but this fact is not often considered. Daborn & Clifford (1974) pointed out that complete freezing results in several physical and chemical effects that are of considerable biological importance.

A rise of conductivity with decreasing water volume during summer drying (Moore 1970; Lake et al. 1989; Serrano & Toja 1995), was not observed in the ponds investigated. With decreasing water volumes in summer 1998 and 1999, the conductivity also drops. Schneider & Frost (1996) also found no increase in conductivity as the ponds dried out and pointed out that this shows that water loss is dominated by seepage rather than evaporation.

Only in the last hydrographic stage were extreme values found. The high conductivity immediately before completely drying out and before refilling was not only the result of concentration effects due to decreased water volume. It seemed also to result from the re-dissolving of mineral salts from the pond soils and the surrounding environment after strong precipitation.

The increased possibility of the oxidation of organic substances during the dry period could be another explanation. BOULTON & BROCK (1999) predict that newly wetted sediments are also likely to release nutrients, causing a brief peak in dissolved macro-nutrients. There was no temporal trend in conductivity of the pond soil samples taken during the 1998 dry period, but there was a positive correlation between residual moisture of the samples and conductivity after controlled rewetting. It is quite possible that conductivity does not adequately detect nutrient release from dried sediments. Winter freezing of the pond soils may have also disruptive effects on the soil and probably promotes nutrient release (DABORN & CLIFFORD 1974). Despite the correlation between variation in volume and change of conductivity for the total investigation period, in some periods stronger correlation's were found. Most especially, conductivity and pond volume were strongly negative correlated in winter due to the effects of cryogenic salting out, and in the refilling phase in autumn 1998. Cryogenic salting out is result of the water crystallization process in which some elements or compounds are not integrated in the crystal structure of the ice and so remain behind in the water. In consequence, the ionic concentration increased in the water under the ice cover. The results for conductivity in the ice agree with those of DABORN & CLIFFORD (1974). Salting out is not entirely complete and with increasing ice cover the proportion of integrated compounds also increased. The effects of cryogenic salting out are of substantial importance in small volume water bodies where, because of the much smaller volume, they give rise to the observed high concentrations compared with larger inland waters (e.g. lakes).

Minimum conductivity values resulted after complete refilling of the ponds in the autumn and after the thaw in the spring. Our results point to the presence of concentration and dilution effects that are modified, however, in the annual cycle by different mechanisms. Vertical gradients seem so far hardly examined, the comparatively small or absent modifications of vertical gradients in reaction to volume fluctuations support the view that concentration and dilution effects supply only an insufficient explanation for the observed modifications of conductivity. Respiration and mineralisation processes, which dominate near the bottom layers seem to be important for the formation of these gradients. Reducing conditions within the area of the mud-water boundary, leads here to increased concentrations of different ions (Fe, P, NH_4 and CO_2) (MORTIMER 1941/1942).

The clear decrease or disappearance of the gradients in the dredged ponds is an important indication for this. Some spot checks were done (unpubl. data), PO_4^{3-}, NO_3^-, NO_2^-, NH_4^+ and the hardness were measured, to determine the ionic composition responsible for the observed conductivity gradients. Only the hardness [$Ca(HCO_3)_2$ and $Mg(HCO_3)_2$] seems to be important because of their considerable differences between surface and bottom, the other components showed no distinct vertical stratification.

It seems that calcium and CO_2 as HCO_3, but also HCO_3^{2-} and free dissolved CO_2, are important for the occurrence of vertical conductivity gradients in the ponds although further components could be also important. The clear reduction of the gradient width in the spring and the "disappearing" of these gradients in the dredged ponds indicate, on the one hand, the increased dissipation of dissolved substances in the spring and show, on the other hand, that the turnover process at the bottom is of substantially importance for the occurrence of these gradients. The increased range of the gradients in winter is certainly influenced by respiration and mineralisation processes and the effects of cryogenic salting.

VAAS & SACHLAN (1955) and GANAPATI (1955) referred to vertical CO_2 gradients with an opposite direction in comparison to the common oxygen gradients (surface $O_2 >$ bottom O_2).

Both authors described a diurnal CO_2 cycle although I found no clear diurnal cycle for conductivity and reference works on such gradients are rare or are missing. More than thirty years ago ERIKSEN (1966) referred to the necessity of sampling vertically, diurnally and seasonally. From the available reports, the type of sampling and the repeated checking of the results lead to the assumption that the effects of additional mechanisms are important in addition to the frequently assumed concentration and dilution. The vertical distribution of materials in small waters represents a poorly examined aspect of their hydrology and the importance of these gradients for the biota is difficult to assess.

Investigations of the seasonal, diurnal modifications and of vertical gradients of the hydrogen ion concentration are present to small extent. KÜHLMANN (1960) observed "a rise of the pH value with the removing of the water levels". HAMER & APPLETON (1991) do not describe considerable trends for the observed fluctuations of the pH value from temporary waters in South Africa. BARCLAY (1966) describes a similar decrease in pH values as drying out progresses for this type of waters. BAZZANTI et al. (1996) found minimum pH values at the beginning and the end of the wet period and they also recorded a positive correlation between pH and maximum depth and area.

The seasonal trends described in the available investigation correspond closely with the results of PETERSEN (1926).

The rise of the pH values in the winter in "ice-free" periods and in spring after the last ice period is probably the effect of increased assimilation by the phytoplankton and the submerged vegetation (KÜHLMANN 1960), as well as by the greater diffusion of carbon dioxide due to the lack of ice cover. After thawing, total CO_2 was reduced and, in particular, free CO_2 nearly disappeared (unpubl. data). In this situation, considerable $CaCO_3$ precipitation can occur. In contrast, snow-covered ice forms an almost opaque layer and limits substantially the photosynthetic activity of submerged vegetation. The formation of H_2S and increased concentrations of total CO_2 and, especially, free CO_2 (unpubl. data) lead to the low pH values in the winter. The observed diurnal cycle and modifications of pH value gradients is comparable to the results of several other authors (GEORGE 1961; MORTON & BAYLY 1977; WHITNEY 1942). The rise of the pH during the day is caused by the photosynthetic activity of the submerged plants and the phytoplankton. The existence and stability of pH gradients in the winter is especially interesting.

The described seasonal modifications of the oxygen saturation and the observation of vertical oxygen gradients are in conformity with KÜHLMANN (1960), COLE & FISHER (1977) and other authors. In winter ice cover forms a diffusion barrier and this leads in phases, in those the ponds were covered with a layer of thin, clear ice, to extreme oxygen super-saturation. Apart from this, oxygen super-saturation was also registered in the spring.

DABORN & CLIFFORD (1974) described that as a consequence of cryogenic salting out with increasing ice cover the water beneath the ice became super-saturated with dissolved oxygen This effect could not be observed in this investigation. In winter phases with thickly snow-covered ice, photosynthetic activity was limited and extreme oxygen deficits occurred.

The diurnal oxygen cycle is comparable with the results of ERIKSEN (1966), GANAPATI (1955), SCHOLNICK (1994), WHITNEY (1942) and VAAS & SACHLAN (1955). In the bottom region it comes to oxygen consumption. Therefore the gradients are similar to that which are found in lakes. Photosynthetic activity is likely to increase oxygen saturation and oxygen gradients during the daytime. During the night, the oxygen saturation decreased and oxygen gradients were reduced because oxygen production does not occur. After refilling, small oxygen deficits occur due to a time lag in the recovery of aquatic vegetation. In both periods (before and after dredging) oxygen content is strongly influenced by the stage of vegetation succession. It seems that in the spring and summer phase, the successional stage has a smaller influence on oxygen conditions than the degree of drying reached in the ponds. The small depth of water, high water temperatures, and drying out of large areas of the ponds substantially impair the growth of the submerged vegetation and the phytoplankton.

A lot of works deal with the topic "temperature in small waters": BAMFORTH (1962), BARCLAY (1966), BEHRENS (1937), GANAPATI (1955), GEORGE (1961), GIEYSZTOR (1934), HAMER & APPLETON (1991), HARTLAND-ROWE. (1966), JOURNEYS (1973), KÜHLMANN (1959, 1960, 1961), MORTON & BAYLY (1977), PICHLER (1939), SCHWABE (1939), VAAS & SACHLAN (1955) and YARON (1964). But most of these papers discuss only the temperature in spring and summer phase.

In agreement with WOODCOCK (1965), the water temperature in winter is strongly influenced by the soil temperature and large inverse stratifications are common. In spring, summer and autumn, direct and inverse gradients are the product of the daily temporal cycle of the ambient soil and air temperatures. Turbidity can also play an important role in the formation of temperature gradients (ANDERSON 1958). The seasonal modifications of turbidity are partially responsible for the variation in light penetration and thus for the formation of temperature gradients. Turbidity leads to greater heating of the layers and limits photosynthesis in the deeper layers (ERIKSEN 1966). In the ponds, submerged and bank vegetation seems to be more important for the formation and the stability of temperature gradients (compare dredged and undisturbed ponds). The close vegetation stands in combination with decreasing water levels reduce the wind-conditioned circulation processes and shaded the deeper layers to a large extent. In the winter the soil temperatures have a large influence on the thermal regime in small waters.

The results suggest that differences in pond size, vegetation succession stage and pond history are related to seasonal, diurnal and vertical variability of many abiotic factors. The size and the temporary character (pond duration) of a pond determine the temporal course of vegetation succession and the persistence of typical stages of vegetation succession. Emergent vegetation influenced the formation and the stability of chemical stratifications and the diurnal cycle of oxygen, pH, and temperature. Pond dredging leads to changes in ponds permanence, vegetation patterns, pond metabolism and pond history. Stratifications of the factors measured were significantly reduced. The pond metabolism was stronger influenced by oxygen production than by decomposition processes (oxygen increased, buffer capacity decreased). This suggests also that beside the emergent vegetation the pond bottom (decomposition processes) is an important factor controlling chemical stratification. In contrast in lakes physical (light, temperature) and chemical stratifications seem to be more a function of the distance between surface and bottom. This seems to be an important difference between small ponds and larger waters.

One important question is how processes in temporary ponds differ from those in permanent ponds (BOULTON & BROCK 1999). COMIN & WILLIAMS (1994) suggest that in temporary ponds, water circulation pattern, nutrient dynamics, and sediment water interactions are essentially the same as in permanent waters but more variable and more closely linked to the ambient environmental conditions. Duration of the dry period and predictability (reliability of filling) are often used as criteria in the classification of temporary wetlands (PAIJMANS et al. 1985; WILLIAMS 1987) and pond duration, in particular, seems to be the major factor controlling the community structure in temporary ponds (SCHNEIDER & FROST 1996). COLLINSON et al. (1995) pointed out that temporary ponds may support particularly distinctive macroinvertebrate assemblages. Loss of water during the drying period may selectively favour invertebrate assemblages dominated by species which have either physical or behavioural attributes to cope with the changes associated with drying (WILLIAMS 1987). Many authors have described several adaptations of organisms in temporary waters [for a review see WILLIAMS (1985) and WILLIAMS (1997)] but the physiological effects of seasonal, diurnal and vertical fluctuations on organisms are largely unknown. Most temporary pond species must have fairly broad tolerances for physical and chemical factors. Some physical and chemical factors and their variations may act as direct signals to organisms and influence decisions for integrating survival strategies (life-history modifications, migration or diapause) at a defined point in time and space.

This study of the physical and chemical factors and of the stage of vegetation succession in temporary ponds was part of a comprehensive investigation. But the first results which are discussed in the present paper are a contribution to fill a gap, because the limnology of temporary waters is poorly documented in comparison to that of larger aquatic ecosystems.

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References

ANDERSON, G. C. (1958): Some limnological features of a shallow saline meromictic lake. Limnol. & Oceanogr. **3**: 259–270.

BAMFORTH, S.S. (1962): Diurnal changes in shallow aquatic habitats. Limnol. & Oceanogr. **7**: 348–353.

BARCLAY, M. H. (1966): An ecological study of a temporary pond near Auckland, New Zealand. Aust. J. Mar. Freshwat. Res. **17**: 239–258.

BAZZANTI, M., BALDONI, S. & SEMINARA, M. (1996): Invertebrate macrofauna of a temporary pond in Central Italy: composition, community parameters and temporal succession. Arch. Hydrobiol. **137** (1): 77–94.

BEHRENS, H. (1937): Temperatur und Sauerstoffuntersuchungen in Tümpeln und Brunnen. Arch. Hydrobiol. **31**: 145-162.

BISHOP, J. A. (1974): The fauna of temporary rain pools in eastern New South Wales. Hydrobiologia **44** (2–3): 319-323.

BONNER, L. A., DIEHL, W. J. & ALTIG, R. (1997): Physical, chemical and biological dynamics of five temporary dystrophic forest pools in central Mississippi. Hydrobiologia **353**: 77–89.

BOULTON, A. J. & BROCK, M. A. (1999): Australian freshwater ecology: Processes and management. Gleneagles Publishing, Adelaide.

BRANDT, A. VON (1937): Das thermische Kleingewässerjahr. Bioklim. Beiblätter, Heft **4**: 32–34.

COLE, J. & FISHER, S.G. (1977): Annual metabolism of a temporary pond ecosystem. The American Midland Naturalist **100**: 15–22.

COLLINSON, N. H., BIGGS, J., CORFIELD, A., HODSON, M. J., WALKER, D., WHITFIELD, M. & WILLIAMS, P. J. (1995): Temporary and permanent ponds: An assessment of the effects of drying out on the conservation value of aquatic macroinvertebrate communities. Biological Conservation **74**: 125–133.

COMIN, F. A. & WILLIAMS, W. D. (1994): Parched continents: our common future? In: MARGALEF, R. (ed.), Limnology now: A paragigm of planetary problems, pp. 473–527. Elsevier, Amsterdam.

DABORN, G. R. & CLIFFORD, H. F. (1974): Physical and chemical features of an aestival pond in western Canada. Hydrobiologia **44** (1): 43–59.

ERIKSEN, C. H. (1966): Diurnal limnology of two highly turbid puddles. Verh. Internat. Verein. Limnol. **16**: 507–514.

GANAPATI, S. V. (1955): Diurnal variations in dissolved gases, Hydrogen ion concentration and some of the important dissolved substances of biological significance in the three temporary rock pools in stream bed at Mettur Dam. Hydrobiologia **7**: 285–303.

GEORGE, M. G. (1961): Diurnal variations in two shallow ponds in Dehli, India. Hydrobiologia **18**: 265–273.

GIEYSZTOR, M. (1934): Limnologische Untersuchungen an einigen Kleingewässern. Arch. Hydrobiol. et Ichthyol. **8**: 75–148.

HAMER, M. L. & APPLETON, C. C. (1991): Physical and chemical characteristics and phyllopod fauna of temporary pools in north-eastern Natal, Republic of South Africa. Hydrobiologia **212**: 95–104.

HARTLAND-ROWE, R. (1966): The fauna and ecology of temporary pools in Western Canada. Verh. Internat. Verein. Limnol. **16**: 577–584.

KÜHLMANN, D. (1959): Wasserführung und Eisverhältnisse zweier Kleingewässer. Acta Hydrophysica **4**: 97–126.

KÜHLMANN, D. (1960): Zur Frage der räumlichen und zeitlichen Verteilung von Sauerstoff und anderen chemischen Faktoren in kleinen Gewässern. Gerlands Beitr. Geophys. **69**: 294–319.

KÜHLMANN, D. (1961): Thermodynamische Untersuchungen in Kleingewässern verschiedener landschaftlicher Exposition. Verh. Internat. Verein. Limnol. **14**: 87–94.

LAKE, P. S., BAYLY, I. A. E. & MORTON, D. W. (1989): The phenology of a temporary pond in western Victoria, Australia, with special reference to invertebrate succession. Arch. Hydrobiol. **115** (2): 171–202.

MOORE, W.G. (1970): Limnological studies of temporary ponds in southern Louisiana. Southwestern Nat. **15**: 83–110.

MORTIMER, C.H. (1941/1942): The exchange of dissolved substances between mud and water in lakes. J. Ecol. **29**: 280–329; Ibid. **30**: 147–200.

MORTON, D. W. & BAYLY, I. A. E. (1977): Studies on the ecology of some temporary freshwater pools in Victoria, Australia with specific reference of mircocrustaceans. Aust. J. Mar. Freshwater Res. **28**: 439–454.

NILSSON, A. N. (1984): Species richness and succession of aquatic beetles in some kettle-hole ponds in northern Sweden. Holarctic Ecology **7**: 149–156.

PAIJMANS, K., GALLOWAY, R.W., FAITH, D.P., FLEMING, P.M., HAANTJENS, H.A., HEYLIGERS, P.C., KALMA, J.D. & LOFFLER, E. (1985): Aspects of Australian Wetlands. CSIRO Div. Land Ware Res. Tech. Pap. No. 44.

PETERSEN, W. (1926): Seasonal succession of animals in a *Chara*-cattail pond. Ecology **7** (3): 371–377.

PICHLER, W. (1939): Unsere derzeitige Kenntnis von der Thermik kleiner Gewässer. Thermische Kleingewässertypen. Internat. Rev. Hydrobiol. **38**: 231–242.

SCHNEIDER, D.W. & FROST, T. M. (1996): Habitat duration and community structure in temporary ponds. J. N. Am. Bethol. Soc. **15** (1): 64–86.

SCHNEIDER, D.W. & FROST, T. M. (1997): Predation and food web structure along a habitat duration gradient. Oecologia (Berlin) **110** (4): 567–575.

SCHOLNICK, D. A. (1994): Seasonal variation and diurnal fluctuations in ephemeral desert pools. Hydrobiologia **294**: 111–116.

SCHWABE, G.H. (1939): Über die Temperaturverhältnisse einiger Gewässer in Westpatagonien. Arch. Hydrobiol. **35**: 469–488.

SERRANO, L. & TOJA, J. (1995): Limnological description of four temporary ponds in the Donana National Park (SW, Spain). Arch. Hydrobiol. **133** (4): 497–516.

STEWART, R. E. & KANTRUD, H.A. (1971): Classification of natural ponds and lakes in the glaciated prairie region. USDI, FWS. Resource Publ. 92, 57 pp.

VAAS, K.F. & SACHLAN, M. (1955): Limnological studies on diurnal fluctuations in shallow ponds in Indonesia. Verh. Int. Verein. Limnol. **12**: 309–319.

WHITNEY, R. J. (1942): Diurnal fluctuations of oxygen and pH in two small ponds and a stream. J. Exp. Biol. **19**: 92–101.

WIGGINS, G. B., MACKAY, R. J. & SMITH, I. M. (1980): Evolutionary and ecological strategies of animals in annual temporary pools. Arch. Hydrobiol. **125**: 85–110.

WILLIAMS, D. D. (1987): The ecology of temporary waters. Timber Press. Portland, Oregon.

WILLIAMS, D. D. (1997): Temporary ponds and their invertebrate communities. Aquatic conservations: Marine and freshwater ecosystems,Vol. 7, pp. 105–107.

WILLIAMS, W. D. (1985): Biotic adaptations in temporary lentic waters, with special reference to those in semi-arid and arid regions. Hydrobiologia **125**: 85–110.

WOODCOCK, A. H. (1965): Melt patterns in ice over shallow waters. Limnol. & Oceanogr., Suppl. **10**: 290–297.

YARON, Z. (1964): Notes on the entomostracan fauna of temporary rainpools of in Israel. Hydrobiologia **24** (4): 489–513.