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Soda pans – jewels of the Nationalpark Neusiedler See-Seewinkel An opinion based on limnological data

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Soda pans are a unique type of inland saline waters in Europe and they are restricted to the Carpathian Basin in Central Europe. Their salinity varies between hyposaline and hypersaline depending on the water level. They are dominated by sodium, hydrocarbonate and carbonate ions. Magnesium sometimes occurs as a secondary dominant cation.
Salinity, ionic composition and zooplankton of seven shallow astatic soda pans east of Neusiedler See, Austria, were studied over a period of five years. The zooplankton communities of the soda pans are mostly dominated by crustaceans (*Arctodiaptomus spinosus*, *Moina brachiata*), but at high conductivity levels rotifers, especially *Brachionus asplanchnoidis* can be the dominant, if not the only plankton organism. Zooplankton biomass and the phenology of the drying up phases are described and discussed.
Although these salt lakes are unique habitats within Europe and many of them are situated in national parks, their conservation status is critical. Especially regional groundwater overexploitation and withdrawal of the surface waters from the area resulted in a more than 80 % reduction of the water surface area in the Seewinkel (Austria) and the Danube-Tisza Interfluve Region (Hungary) by the end of the 20th century.
Predictions concerning climatic changes in the Carpathian Basin warn about the increased occurrence of extreme climatic phenomena. As a consequence, climatic water deficiency is expected.

Herzig A., 2020: Sodalacken – Juwele des Nationalparks Neusiedler See-Seewinkel. Eine Ansicht basierend auf limnologischen Daten.
Sodalacken sind einzigartige Binnensalzgewässer, die in Zentraleuropa vor allem im Karpatenbecken vorkommen. Ihre Salinität reicht von hyposalin bis hypersalin, je nach dem ob die Lacken frisch mit Regenwasser befüllt sind, oder sich in der Phase der Abtrocknung befinden. Die Ionenzusammensetzung dieser Gewässer wird von Natrium, Hydrogenkarbonat und Karbonat bestimmt, in manchen Fällen ist Magnesium das zweithäufigste Kation.
Über einen Zeitraum von fünf Jahren wurden elektrische Leitfähigkeit (Salinität), Ionenzusammensetzung und das Zooplankton von sieben Salzlacken östlich des Neusiedler Sees untersucht. Das Zooplankton der Lacken bestand zumeist aus Crustaceen (dem Copepoden *Arctodiaptomus spinosus* und der Cladocere *Moina brachiata*), aber wenn die Gewässer hohe Leitfähigkeiten aufwiesen bildetet die Rotifera, vor allem *Brachionus asplanchnoidis*, die Hauptmasse des Bestandes. Zooplanktonbiomasse und die Phänologie der Abtrocknungsphasen werden beschrieben und diskutiert.
Obwohl diese Salzgewässer einzigartige Lebensräume in Europa darstellen und viele in Nationalparks liegen, muß ihr Erhaltungszustand als kritisch beurteilt werden. Regionale, außerordentlich hohe Grundwasserentnahmen und Ableitung der Oberflächengewässer führte bis zum Ende des 20. Jahrhunderts zu einer Reduktion der Wasserflächen der Lacken um 80 % im Seewinkel und im Donau-Theiß-Zwischenstromland. Prognosen zu den Auswirkungen des Klimawandels im Karpatenbecken warnen vor extremen Klimaphänomenen, als eine Konsequenz daraus wird zukünftig Wassermangel in dieser Region erwartet.

Keywords: athalassic saline, conductivity, salinity, zooplankton biomass, drying up phases, *Brachionus asplanchnoidis*, *Arctodiaptomus spinosus, Moina brachiata*.

Introduction

Athalassic (inland) saline lakes occur in dry climate zones on every continent. They tend to occur in endorheic drainage basins where evaporation exceeds precipitation. These saline waters are defined as those having salinities equal to, or higher than 3 g.L^{-1} salinity. Freshwater lakes have 0,5 g.L^{-1} or less dissolved salts, hyposaline lakes have 3–20 g.L^{-1}, mesosaline 20–50 g.L^{-1} and hypersaline more than 50 g.L^{-1} (Hammer 1986). Hutchinson (1957) states that the salinity of an inland water may be regarded as the concentration of all ionic constituents present. That is also used by Hammer (1986), salinity is the sum of the eight major ions, i.e. sodium (Na), potassium (K), magnesium (Mg), calcium (Ca), chloride (Cl), sulphate (SO_4), hydrocarbonate (HCO_3), carbonate (CO_3). Athalassic saline waters are divided into three extreme types based on the dominance of the anions: carbonate (including bicarbonate), chloride, sulphate. Most common among world saline lakes are the chloride waters, sulphate dominated lakes are mostly found in North America and Asia and in Austria – Herrnsee (Hammer 1986). Sodium is by far the dominant cation, magnesium ist the second most prominent cation.

We find large permanent lakes like the Great Salt Lake (USA), Lake Balkash (Kazakhstan), very deep saline lakes like Van Gölü (Turkey), the Dead Sea (Israel/Jordan), the Issyk-kul (Kirgizia), Lake Shala (Ethiopia), or very large shallow lakes as Lake Eyre (Australia), Lake Niriz (Iran), Lake Natron (Tanzania) (Melack 1983, 2002, Williams 1996). However, most saline waters are small in size, shallow and may be ephemeral and for these the term „pan" is used (Hutchinson et al. 1932).

In the arid, continental zone of Eurasia the easternmost soda pans can be found in Manchuria, the westernmost are situated in the Carpathian Basin (Löffler 1971). These soda pans are a unique type of inland saline waters in Europe. Most of the lakes found in the Hungarian Plain, eastern Austria (Seewinkel) and Serbia are carbonate waters and all of these lakes have sodium associated as the major cation (Boros et al. 2013, 2014). Salinity ranges between subsaline (0,5–3 g.L^{-1}) and hypersaline (>50 g.L^{-1}). Altogether 77 salt pans without any anthropogenic disturbance were described by Boros et al. (2013). 32 of these undisturbed pans are located east of Neusiedler See (Austria), in an area of about 200 km^2 called „Seewinkel" (lake district).

Their ionic composition is similar to other alkaline lakes in e.g. China, Mongolia, Middle-Asia, East Africa, North America or Australia (Hammer 1986, Boros et al. 2013, Schagerl 2016). Besides alkalinity the soda pans show a great degree of turbidity caused by suspended particles and frequently a high concentration of dissolved humic substances. Most of them are astatic, they dry out seasonally. Saline lake surface levels tend to fluctuate considerably both seasonally and annually, they vary in salinity and water chemistry following the meteorological situation. Soda lakes represent naturally occurring highly alkaline environments, often exhibiting pH-values >11,5 (Grant 2006).

Research on Austrian and Hungarian saline lakes has been carried out since more than 100 years. Most investigations were small-scale studies (in time and/or in space). One of the earliest papers on the microfauna of the sodic waters from Hungary was published by Daday (1893). Later, Nógrádi (1957) gave a description of the limnology and the rotifer fauna of Hungarian sodic waters. Papers by Megyeri (1959, 1963, 1971, 1975) present the results of investigations of the zooplankton (Rotifera and Crustacea) of the sodic waters. A review about the research so far was presented by Ponyi (1961). Extensive studies on geology, phytoplankton, zooplankton and zoobenthos were carried out on the Fülöpháza pans between 1972 and 1974 (Molnár 1976, Kiss 1975, Megyeri 1975, Ferencz 1976). Since 1978 L. Forró has studied rotifers and crustaceans from the saline lakes in the Carpathian Basin (Forró & Ronkay 1983, Forró 1988, 1989, 1992, Baranyai et al. 2004). Since the 1990 ies E. Boros has initiated numerous studies on the saline lakes of the Carpathian Basin. One topic of the research was the ionic composition and salinity of the pans. On the basis of new data and archive data he found a high chemical diversity of alkaline soda pans in the Carpathian Basin (Boros et al. 2014). A special focus was put on the trophic web in these saline systems and especially on the role of aquatic birds as top consumers (Boros et al. 2006 a, b, Boros 2007, Boros et al. 2008 a, b). The effect of different invertebrate food types on the habitat choice and distribution of waterbird species on 82 pans in the Carpathian Basin was demonstrated by the investigation of Horváth et al. (2013). Another large scale study was performed by Tóth et al. (2014). The authors sampled 110 soda pans in the Carpathian Basin and analyzed the zooplankton composition including rotifers, copepods and cladocerans in spring and summer.

Most of the efforts put into the investigation of the salt pans resulted in the book „Ecology and Management of Soda Pans in the Carpathian Basin“ (Boros et al. 2013). In this book one can find a general description of soda pans, a detailed description of all the surveyed soda lakes (77 natural soda pans, 66 soda pans affected by anthropogenic disturbance, 5 restored or rehabilitated pans) and examples and suggestions for management, rehabilitation and restoration of the pans. Recently two reviews were published. One on defining chemical properties of soda lakes based on data fro Eurasian saline surface waters (Boros & Kolpakova 2018) and one on microbial communities of soda lakes and pans in the Carpathian Basin (Felföldi 2020).

In Austria one of the early papers was published by Stundl (1938). From spring 1936 until summer 1937 the author performed limnological investigations analyzing chemical, biological and microbiological samples from 3 pans near Illmitz (Silberlacke, Runde Lacke, Einsetzlacke). Chemical analyses and an investigation of the diatoms were done by Legler (1941) and crustaceans were studied by Pesta (1937). Two basic papers were contributed by Löffler in the 1950s, investigating the chemical composition of the waters and the rotiferan and crustacean communities of 56 pans in December 1956, April, June and October 1957, and June, July and November 1958 (Löffler 1957, 1959). Papers from the 1960s and 1970s dealt with specific topics (e.g. limnology of a few pans – Peschek 1961, chemistry – Knie 1961, Knie & Gams 1962, ciliates – Dietz 1963, rotifers – Ruttner-Kolisko 1971, Birnbaumlacke – Jungwirth 1973, Newrkla 1974, and Glatz 1976, or amphibians – Fischer-Nagel 1977, and the landscape – Löffler 1982).

An analysis of chemistry and crustacean zooplankton was performed by Metz & Forró (1989, 1991) between May 1982 and May 1985. Their comparison with earlier data revealed some changes in chemistry and zooplankton, but they also pinpoint the losses of many smaller pans as a result of human activities mainly impacts into their hydrology. From the beginning of the 20th century wide spread artificial draining took place which withdrew the surface waters very effectively and also lowered the water table. In addition, long-term extraction of groundwater for irrigation exceeded long-term recharge rates leading to regional groundwater overexploitation. Altogether this management in the Seewinkel caused severe damage to the natural hydrological cycle and to the aquatic ecosystems (Herzig 1994).

In the 1990s and beginning of 2000 valuable contributions on water budget and chemistry were published by Krachler (1992) and Krachler et al. (2000) and bacterial and cyanobacterial numbers as well as heterotrophic production of selected pans were examined by Kirschner et al. (2002) and Eiler et al. (2003). A basic survey on the zoobenthic community of the Austrian salt pans was performed by Wolfram et al. (1999, 2004). In September 2002, December 2002 and May 2003 a survey on flagellates and ciliates was performed in selected shallow saline pans within the area of the Nationalpark Neusiedler See/Seewinkel (Zimmermann-Timm & Herzig 2006).

As a great number of saline pans vanished within the last decades and the threatening scenarios of human impact still remained, an ecological evaluation of 59 Austrian pans was performed, the restauration potential defined, and restauration measures suggested (Krachler et al. 2012).

Nowadays the Nationalpark Neusiedler See-Seewinkel in cooperation with the Biological Station Neusiedler See performs a chemical and biological monitoring of the salt pans.

Differences in zooplankton communities have been observed among lakes with different ionic composition (Williams et al. 1990) and the inverse relationship between salinity in saline lakes and zooplankton species richness is well known and often documented (e.g. Löffler 1961, Green 1986, 1993, Hammer 1986, 1993, Metz & Forró 1989, Williams et al. 1990, Horvath et al. 2013). However, little is known about the sequential response of zooplankton communities to changing salinity and chemical composition in individual lakes.

This study reports the hydrological and chemical characteristics of seven saline pans for the years 2010–2014 and provides an account of the pans rotifer and crustacean community and their association with changing salinity, with special focus on the drying up phases of the pans. Furthermore, an estimation of the zooplankton biomass development over the five years is presented, seen as a basic food resource for waterbirds.

Materials and methods

Since 2008 the Austrian salt pans were visited by the author in a varying time schedule and samples for chemical and biological analyses were taken. In this paper results for seven pans, Albersee (8,8 ha), Illmitzer Zicksee (54 ha), Obere Halbjochlacke (23,1 ha), Obere Hölllacke (6,5 ha), Oberer Stinkersee (49,5 ha), Runde Lacke (3,3 ha) and Unterer Stinkersee (35,1 ha) are presented (the area indicated is the potential water surface area) (Fig. 1).

Between 2010 and 2014 seven soda pans were sampled on average biweekly (24 times a year; range: 15–36 times), mostly between 2 p.m. and 4 p.m. Ten litres of water were randomly collected from a wide area in the open water of each pan by a scoop. Out of this pooled sample two litres were brought to the laboratory and sieved through a 30 µm mesh plankton net. The filtrate was preserved in 4 % formalin. All large items (Anostraca, Corixidae, Ceratopogonidae and other insect larvae) were picked out of the sample. All zooplankton organisms were counted in an inverted microscope. *Arctodiaptomus spinosus* (Daday, 1891) was differentiated into adult male, adult female, copepodids and nauplii, in the case of *Daphnia magna* Straus, 1820 and *Moina brachiata* (Jurine, 1820) adult and juveniles were counted. Additionally, subitaneous and resting eggs were counted. All counts were expressed as individuals per litre. After the identification of the species and count-

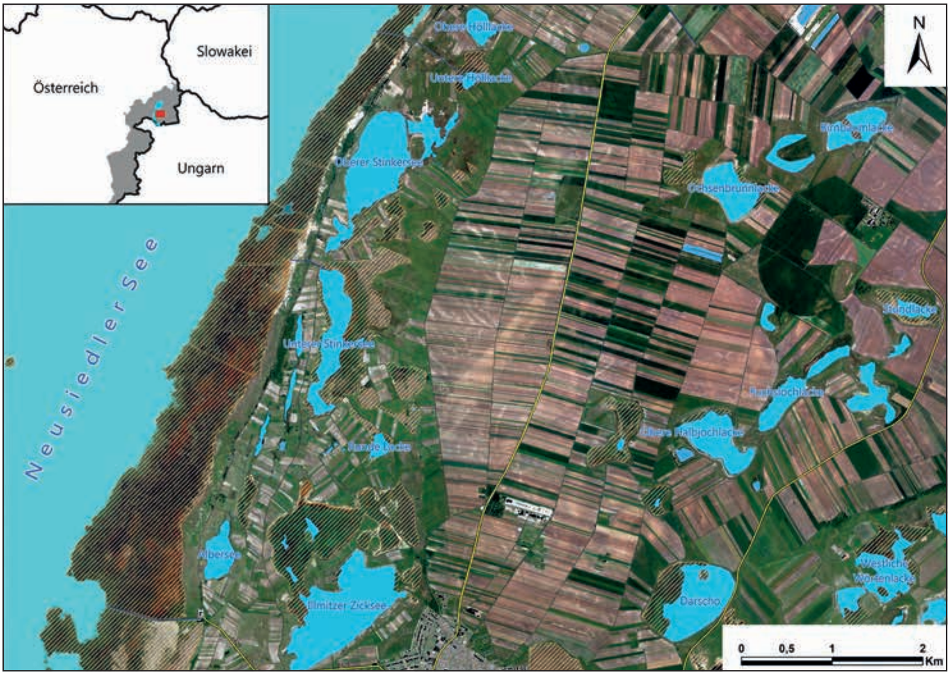

Fig. 1: Map of the investigation area east of Neusiedler See; blue area of the pans = potential open water area. – Abb. 1: Karte des Untersuchungsgebietes östlich vom Neusiedler See; blaue Fläche der Lacken = potentielle Wasserfläche.

ing total biomass of zooplankton was determined by filtering the sample through a 100 µm mesh plankton net, rinsing it with distilled water and drying the filtrate in pre-dried ceramic pans at 100° C for 12 hours. After cooling in a desiccator the dried material was weighed on a Mettler Toledo XS 205 Dual range electronic microbalance.

The chemical analyses were performed by the certified laboratory of the Biological Station Neusiedler See in the context of a routine monitoring covering the years 2008–2011. Temperature and electrical conductivity were measured in situ with a WTW Cond 315i electrode and oxygen and pH with a HACH HQ 40 d electrode at the time of each collection.

Results

Limnological parameters as background information

The seven pans were varying in size (3,3–54 ha), but generally rather small. Their average depth was less than 25 cm. As considerable wind was present most of the time, they were polymictic and no stratification was detected. In Figure 2 all water temperatures measured at the day and time of sampling are plotted. As sampling was performed between 14:00 and 16:00 one can assume that these records resemble maximum temperatures on the particular day. Between end of May and mid-September most of the readings were above 25° C, and from the second half of June until mid-August temperatures were above 30° C. The highest temperature measured was 37° C. Beside the high temperatures during day time,

Tab. 1: Ionic composition of the investigated pans (salt lake); data from the years 2008–2011; n = number of sampling dates (data: certified laboratory of the Biological Station Neusiedler See). – Tab. 1: Ionenzusammensetzung der untersuchten Lacken; Daten aus den Jahren 2008–2011; n = Anzahl der Untersuchungen (Datenquelle: Labor Biologische Station Neusiedler See).

Salt lake	conductivity mS cm^{-1}	alkalinity meq.L^{-1}	pH	Na	K	Ca	Mg	Cl	CO_3+HCO_3	SO_4
						mg.L^{-1}				
Albersee (n = 24)	3,59–46,2	83,06	9,53	5865,7	195,8	24,3	108,6	2173,4	2860,2	3603,9
Illmitzer Zicksee (n = 16)	1,34–7,63	19,55	9,23	691,4	43,2	30,8	43,2	247,8	1091,9	348,3
Runde Lacke (n = 8)	3,1–13,8	43,68	9,41	1884,2	63,6	16,9	46,9	466,1	2378,1	1374,0
Unterer Stinkersee (n = 40)	2,27–17,0	63,0	9,30	1944,3	58,6	17,8	82,9	490,0	3343,6	947,8
Oberer Stinkersee (n = 25)	1,43–26,2	71,77	9,35	2832,7	74,9	51,3	38,1	609,5	3923,6	1174,4
Obere Hölllacke (n = 4)	3,1–9,2	41,40	9,25	1474,0	34,2	22,0	31,2	438,5	2252,5	1034,5
Obere Halb-jochlacke (n = 37)	1,32–33,3	118,87	9,41	6298,2	27,0	15,2	26,3	723,1	6152,9	3407,6

Tab. 2: Dissolved organic carbon (DOC), total phosphorus (P_{tot}) and Chorophyll a (Chla) of the investigated pans (salt lakes); data from the years 2008–2011; mean and in parenthesis standard deviation; n = number of sampling dates (data: certified laboratory of the Biological Station Neusiedler See). (Calculations were performed with log-transformed values). – Tab. 2: Gelöster organischer Kohlenstoff (DOC), Gesamtphosphor (P_{tot}) und Chorophyll a (Chla) der untersuchten Lacken; Daten aus den Jahren 2008–2011; Mittelwert und in Klammer Standardabweichung; n = Anzahl der analysierten Proben (Datenquelle: Labor Biologische Station Neusiedler See). (Berechnung mit log-transformierten Werten).

Salt lake	DOC mg.L^{-1}	P_{tot} mg.L^{-1}	Chla µg.L^{-1}
Albersee (n = 11)	67,0 (135,5 – 33,1)	1,41 (2,83 – 0,7)	43,8 (146,6 – 13,1)
Illmitzer Zicksee (n = 22)	38,1 (66,2 – 21,9)	0,2 (0,53 – 0,08)	11,6 (93,8 – 1,4)
Runde Lacke (n = 10)	58,1 (90,2 – 37,4)	0,18 (0,32 – 0,1)	13,3 (60,7 – 2,9)
Unterer Stinkersee (n = 18)	51,5 (80,0 – 33,2)	0,12 (0,22 – 0,07)	6,8 (12,1 – 3,9)
Oberer Stinkersee (n = 21)	32,4 (75,2 – 13,7)	2,36 8,02 – 0,69)	42,5 (117,5 – 15,3)
Obere Hölllacke (n = 10)	45,9 (48,6 – 43,4)	2,06 (5,16 – 0,83)	26,7 (71,6 – 9,9)
Obere Halbjochlacke (n = 14)	15,8 (28,5 – 8,8)	1,81 (4,06 – 0,81)	38,2 (105,2 – 13,9)

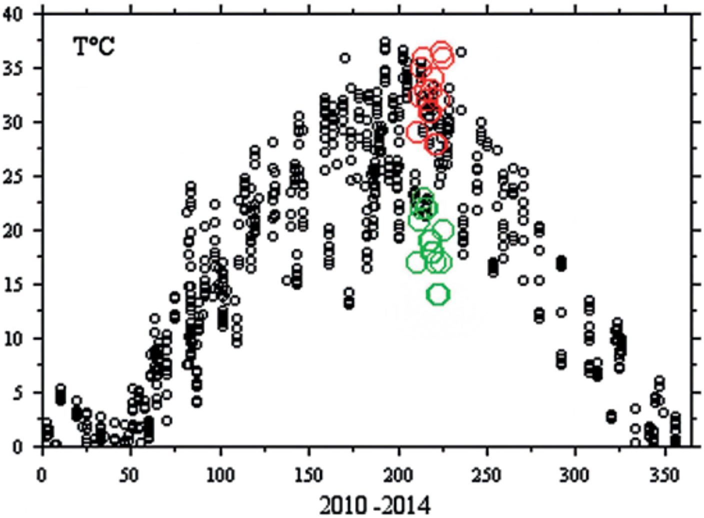

Fig. 2: Water temperature measurements 2010–2014, black circles: measurement on the actual sampling days, daily variation is indicated for the period of 30.07.–13.08., red circles: maxima, green circles: minima (readings from the meteorological station Unterer Stinkersee, Biological Station Neusiedler See). – Abb. 2: Wassertemperatur 2010–2014, schwarze Kreise: aktuelle Messungen zum Sammelzeitpunkt, Tagesschwankungen sind für die Periode 30.07.–13.08. eingezeichnet, rote Kreise: Tagesmaxima, grüne Kreise: Tagesminima (Aufzeichnungen der meteorologischen Station Unterer Stinkersee, Biologische Station Neusiedler See).

the lakes were characterized by a well expressed difference between day and night temperatures which may reach 10–19° C (red and green circles in Fig. 2, readings from the meteorological station Unterer Stinkersee, Biological Station Neusiedler See).

The average dissolved oxygen saturation was 120 % (SD 31,5 %), with maxima being far above 200 %. At dawn very low saturations were found (<20 % saturation).

The main chemical characteristics are summarized in Table 1. The average pH of the pans was 9,4 (SD 0,4). The ionic composition revealed a clear dominance of sodium, carbonate and hydrogencarbonate ions. Sodium was the dominant cation, with considerable contribution of magnesium in some of the pans (e.g. Albersee). According to the results of the chemical composition, analysed for a wide range of conductivities, six pans clearly belonged to the most frequent type of soda water, the Na-HCO_3 alkaline type, only the data for Albersee showed in addition to the dominant sodium a higher value for Mg and nearly equal contribution of the anions CO_3+HCO_3, SO_4 and Cl. Although the salt concentrations varied considerably during the period of investigation, the ionic proportions showed a remarkable constancy.

For comparison with other studies conductivity was converted to salinity or alkalinity by applying the following equations derived from the chemical analyses and the conductivity measurements: alkalinity – meq.L^{-1}, total ions – mg.L^{-1}, conductivity – mS.cm^{-1}

Equations for the pans Obere Halbjochlacke, Oberer Stinkersee and Obere Hölllacke:
total ions = 0,367 + 0,698 cond + 0,02 cond^2; r^2 = 0,986; P < 0,0001; n = 45
alkalinity = 3,988 + 5,766 cond + 0,148 cond^2; r^2 = 0,993; P < 0,0001; n = 51

Equations for the pans Albersee, Illmitzer Zicksee and Runde Lacke:
total ions = -0,241 + 0,802 cond + 0,007 cond^2; r^2 = 0,987; P < 0,0001; n = 45
alkalinity = 6,114 + 3,716 cond + 0,073 cond^2; r^2 = 0,986; P < 0,0001; n = 50

In Table 2 data for dissolved organic carbon (DOC), total phosphorus (P_{tot}) and Chlorophyll a (Chla) are summarized. The highest DOC values were measured in pans with established *Phragmites* stands along the shore. Maxima of 236 mg.L^{-1} and 168 mg.L^{-1} were found in Oberer Stinkersee and Albersee respectively. Albersee, Runde Lacke and Unterer Stinkersee revealed the highest average values, 67 mg.L^{-1}, 58,1 mg.L^{-1} and 51,5 mg.L^{-1} respectively.

In four of the seven pans studied the mean total phosphorus values were in the milligramme range (Tab. 2). The average P_{tot} for the investigation period varied between 0,12 mg P_{tot}.L^{-1} (Unterer Stinkersee) and 2,36 mg P_{tot}.L^{-1} (Oberer Stinkersee). The maxima measured reached 12,6 mg P_{tot}.L^{-1} and 20 mg P_{tot}.L^{-1} in Oberer Stinkersee.

The mean Chla values for the seven pans ranged between 6,8 µg.L^{-1} and 43,8 µg.L^{-1} (Tab. 2). The maxima measured were 485,4 µg.L^{-1} (Oberer Stinkersee), 476,4 µg.L^{-1} (Illmitzer Zicksee) and 349 µg.L^{-1} (Albersee).

Precipitation, electric conductivity, zooplankton biomass

The years investigated were quite different with respect to the annual precipitation. The years 2010 (676,8 mm), 2013 (660 mm) and 2014 (712,4 mm) could be called rather wet years, 2012 (607,1 mm) an average year and 2011 (450,5 mm) a rather dry year.

In 2010 none of the seven pans dried up. Highest conductivities were reached by July/August, with 33,1 mS.cm^{-1} in Albersee and between 15 mS.cm^{-1} and 21 mS.cm^{-1} in Runde Lacke, Obere Hölllacke, Obere Halbjochlacke and Oberer Stinkersee. The lowest conductivity was measured in Unterer Stinkersee with values below 5 mS.cm^{-1} (Fig. 3).

The biomass showed in all pans a spring peak (in May) with values between 7 and 17 mgdw.L^{-1}.The highest values were found in Runde Lacke (16,8 mgdw.L^{-1}), Obere Hölllacke (15,9 mgdw.L^{-1}) and Oberer Stinkersee (13,3 mgdw.L^{-1}). The contributing species were different. In Runde Lacke more than 70 % was contributed by *Daphnia magna*, whereas in Oberer Hölllacke and Oberer Stinkersee *Moina brachiata* and *Arctodiaptomus spinosus* built up the biomass.

The highest biomass values were reached during the period of highest conductivities (above 20 mS.cm^{-1}), the maximum was 60 mgdw.L^{-1} in Albersee with just *Brachionus asplanchnoidis* Charin, 1947 present. The highest biomass in Oberer Hölllacke (23,6 mgdw.L^{-1}) was formed by *A. spinosus*, in Illmitzer Zicksee (22,7 mgdw.L^{-1}) and Oberer Stinkersee (15,3 mgdw.L^{-1}) *M. brachiata* and *A. spinosus* revealed these high values.

The lowest biomass was measured in Unterer Stinkersee with values <1 mgdw.L^{-1}, except end of May, when *D. magna* and *A. spinosus* developed a biomass of 8,4 mgdw.L^{-1}.

In 2011, after a winter with very low precipitation of 54,1 mm (December 2010 – February 2011), a dry year with annual precipitation of 450,5 mm followed and Albersee (three times) and Oberer Stinkersee (two times) dried up completely, the other pans did not. In winter and spring in all pans conductivities between 4 mS.cm^{-1} and 10 mS.cm^{-1} were measured. During the final days of drying up Albersee and Oberer Stinkersee reached high-

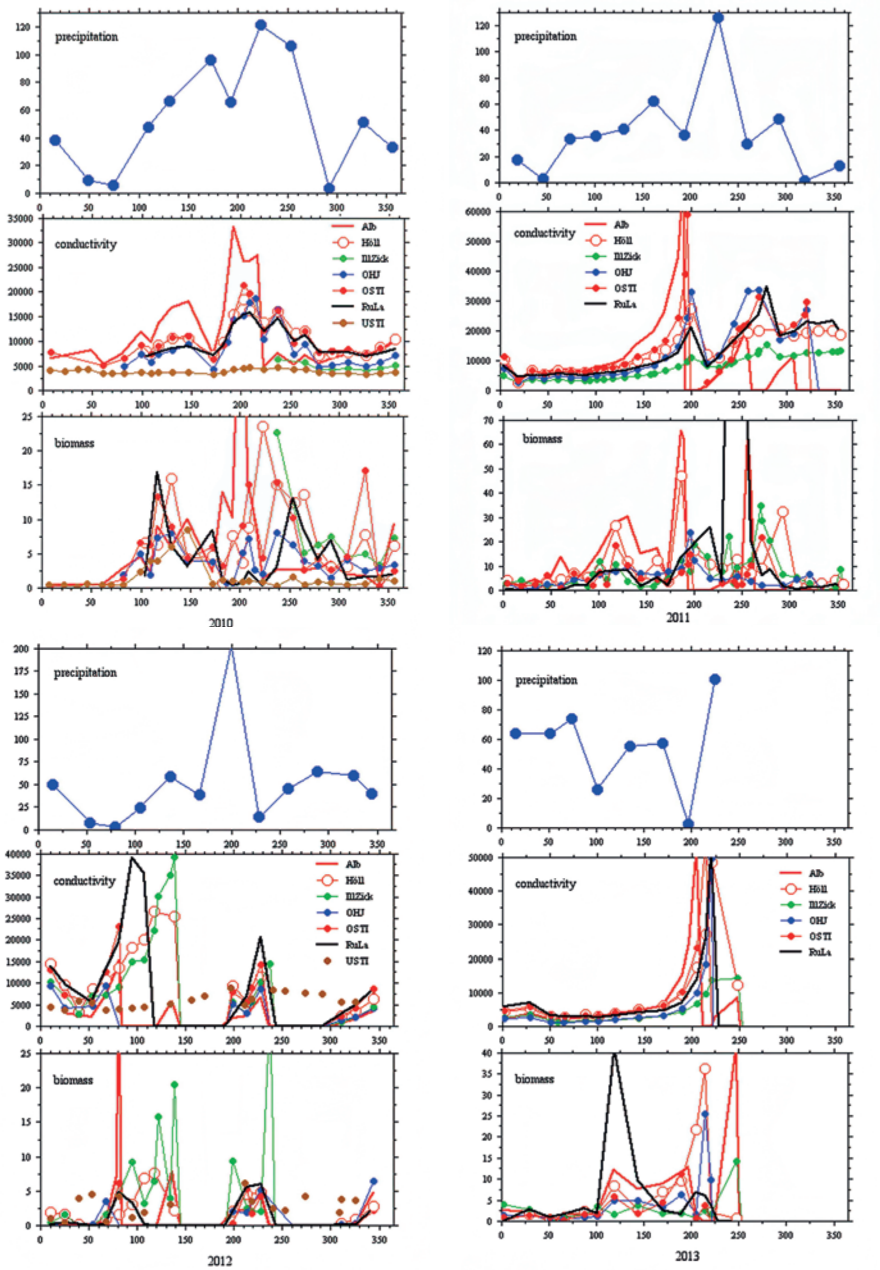

Fig. 3: 2010, 2011, 2012 and 2013. Precipitation per month (mm); electric conductivity ($\mu S.cm^{-1}$); zooplankton biomass ($mgdw.L^{-1}$); x-axis: Julian day; Alb: Albersee, Höll: Obere Hölllacke, IllZick: Illmitzer Zicksee, OHJ: Obere Halbjochlacke, OSTI: Oberer Stinkersee, RuLa: Runde Lacke, USTI: Unterer Stinkersee. – Abb. 3: 2010, 2011, 2012 und 2013. Niederschlag pro Monat (mm); elektrische Leitfähigkeit ($\mu S.cm^{-1}$); Zooplanktonbiomasse ($mgdw.L^{-1}$); x-Achse: Tag, Julianischer Kalender; Alb: Albersee, Höll: Obere Hölllacke, IllZick: Illmitzer Zicksee, OHJ: Obere Halbjochlacke, OSTI: Oberer Stinkersee, RuLa: Runde Lacke, USTI: Unterer Stinkersee.

est conductivities of 95,2 mS.cm^{-1} and 59,0 mS.cm^{-1} respectively. In September, Obere Halbjochlacke, Oberer Stinkersee and Runde Lacke reached conductivities >30 mS.cm^{-1} (Fig. 3).

Like in 2010, a spring peak of biomass showed up in April/May 2011. Albersee reached 30,2 mgdw.L^{-1} and Obere Hölllacke 26,6 mgdw.L^{-1}, with *D. magna*, *M. brachiata* and *A. spinosus* prevailing. In Oberer Stinkersee *M. brachiata* and *B. asplanchnoidis* formed 14,9 mgdw.L^{-1}.

In the final drying up phase (June/July) in Albersee a biomass of 65,6 mgdw.L^{-1} was the result of the development of *B. asplanchnoidis* and in Obere Hölllacke 47,2 mgdw.L^{-1} was mainly due to *A. spinosus*. In August the highest biomass ever measured during this study developed in Runde Lacke; it was the result of a mass development *B. asplanchnoidis* of 298 mgdw.L^{-1}.

In September/October some more biomass peaks developed, 34,8 mgdw.L^{-1} in Illmitzer Zicksee (mainly *B. asplanchnoidis* and *M. brachiata*) and 32,2 mgdw.L^{-1} in Oberer Hölllacke (*A. spinosus* and *B. asplanchnoidis*).

2012 (Fig. 3) was an average year with respect to annual precipitation, but the water situation in the pans was the result of a dry winter 2010/2011 (54,1 mm), a dry year 2011 (450,5 mm) and again a dry winter 2011/2012 (71,0 mm). The conductivity for the winter months was already in a range of 3,6 mS.cm^{-1} (Oberer Stinkersee) – 12,8 mS.cm^{-1} (mean for the seven pans: 7,8 mS.cm^{-1}), which is much higher than the winter conductivity of the other years (2,4–6,8 mS.cm^{-1}; mean: 4,2 mS.cm^{-1}). From January until April only 86,2 mm rain contributed to the water balance and hence, throughout 2012 the pans, except Unterer Stinkersee, did dry up two times, the first drying took place between March 20th and May 25th. The highest conductivities were measured for Illmitzer Zicksee and Runde Lacke (39,2 mS.cm^{-1}). During this phase of steadily increasing conductivity the highest biomass developed; 33,3 mgdw.L^{-1} in Albersee with *A. spinosus* being the species contributing most, 15,8 mgdw.L^{-1} and 20,4 mgdw.L^{-1} in Illmitzer Zicksee, *B. asplanchnoidis* and *A. spinosus* were responsible for the biomass built up. After a dry phase of about 50 days the pans filled again after precipitation of 202,4 mm in July, and during the following drying phase conductivities of 15–20 mS.cm^{-1} were reached. In this period a biomass of about 5 mgdw.L^{-1} was measured, two values from Illmitzer Zicksee were outstanding, 9,4 mgdw.L^{-1} being formed by *B. asplanchnoidis*, *B. leydigii* Cohn, 1862 and *Hexarthra* sp., and 33,6 mgdw.L^{-1} resulting from adults of *A. spinosus*.

After a winter precipitation of 167,3 mm the pans were more or less well filled in 2013 and the drying up started with beginning of July, when monthly precipitation dropped to 3 mm (Fig. 3). Except Unterer Stinkersee the pans dried up. Until end of June conductivities ranged between 2,9 and 5 mS.cm^{-1}. In this period spring biomass maxima were measured, ranging from 5 to 12 mgdw.L^{-1} (Obere Halbjochlacke, Oberer Stinkersee, Obere Hölllacke, Albersee) and an outstanding value of 40,9 mgdw.L^{-1} in Runde Lacke. Above all *D. magna* contributed to these biomass values. In July/August, at the end of the drying up phase the highest conductivities measured varied between 56 mS.cm^{-1} (Oberer Stinkersee) and 48,6 mS.cm^{-1} (Obere Hölllacke). Highest biomass values reached were 25,5 mgdw.L^{-1} (Obere Halbjochlacke), 36,2 mgdw.L^{-1} (Obere Hölllacke) and 41,6 mgdw.L^{-1} (Albersee), the top contributing species was *A. spinosus* and to a lesser extent *M. brachiata*.

Phenology of drying up phases – the main players

Albersee

2010 the pan did not dry up, but two periods of high conductivities occurred (Fig. 4); one in April/May with the highest value being 18 $mS.cm^{-1}$ (salinity: 16,4 $g.L^{-1}$) and a second one in July/August with a maximum of 33,1 $mS.cm^{-1}$ (salinity: 34 $g.L^{-1}$). The daily increase in conductivity was 1,23 $mS.cm^{-1}$. Both periods were characterized by the rapid development of *B. asplanchnoidis*, the density of animals reached $10 \times 10^3.L^{-1}$ and $204 \times 10^3.L^{-1}$. The duration of this population development lasted 10 to 14 days. Before the spring peak of *B. asplanchnoidis*, at conductivities between 7 and 15 $mS.cm^{-1}$, higher numbers of *A. spinosus* (1200 $ind.L^{-1}$, mainly nauplii hatching out of resting eggs) and *M.brachiata* (1300 $ind.L^{-1}$) developed. The autumn zooplankton was dominated by all developmental stages of *A. spinosus*.

In 2011, 3 drying up phases developed. From January until beginning of May conductivity varied between 5 and 12 $mS.cm^{-1}$ and *A. spinosus*, *D. magna* and *M. brachiata* dominated the zooplankton, total abundance reached 2000 $ind.L^{-1}$ (Fig. 5). End of May the first drying up phase started and conductivity increased from 26,1 $mS.cm^{-1}$ (salinity: 25,5 $g.L^{-1}$) to 95,2 $mS.cm^{-1}$ (salinity:139,5 $g.L^{-1}$), which means a daily rate of increase of 3,6 $mS.cm^{-1}$ (salinity: 2,8 $g.L^{-1}$). Seven days before the pan was falling dry *A. spinosus* reached a density of 2400 $ind.L^{-1}$, mainly adults producing resting eggs, at a conductivity of 59 $mS.cm^{-1}$ (salinity: 71 $g.L^{-1}$). The last week a high mortality of *A. spinosus* was noticed. On the other hand, *B. asplanchnoidis* reached a concentration of 172×10^3 $ind.L^{-1}$ in the week before complete dryness of the pan. Although the increase from

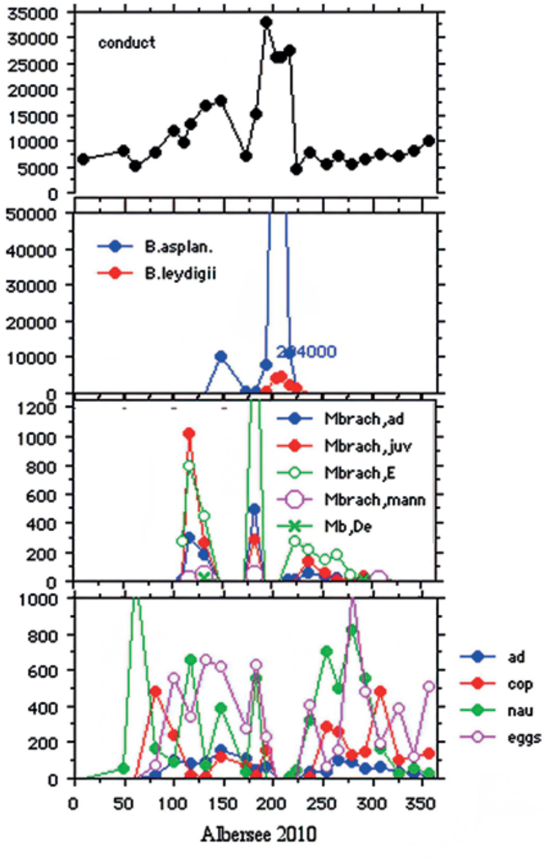

Fig. 4: Albersee 2010. Conduct: electric conductivity ($\mu S.cm^{-1}$); B. asplan: *Brachionus asplanchnoidis* ($ind.L^{-1}$), B. leydigii: *Brachionus leydigii* ($ind.L^{-1}$); Mbrach: *Moina brachiata,* ad: adults ($ind.L^{-1}$), juv: juveniles ($ind.L^{-1}$), E: $eggs.L^{-1}$, mann: male ($ind.L^{-1}$), De: $ephippia.L^{-1}$; *Arctodiaptomus spinosus*, ad: adults ($ind.L^{-1}$), cop: copepodides ($ind.L^{-1}$), nau: nauplii ($ind.L^{-1}$), eggs: $eggs.L^{-1}$. – Abb. 4: Albersee 2010. Conduct: Leitfähigkeit ($\mu S.cm^{-1}$); B. asplan: *Brachionus asplanchnoidis* ($ind.L^{-1}$), B. leydigii: *Brachionus leydigii* ($ind.L^{-1}$); Mbrach: *Moina brachiata,* ad: Adulte ($ind.L^{-1}$), juv: Juvenes ($ind.L^{-1}$), E: $Eier.L^{-1}$, mann: Männchen ($ind.L^{-1}$), De: $Ephippien.L^{-1}$; *Arctodiaptomus spinosus*, ad: Adulte ($ind.L^{-1}$), cop: Copepodid ($ind.L^{-1}$), nau: Nauplien ($ind.L^{-1}$), eggs: $Eier.L^{-1}$.

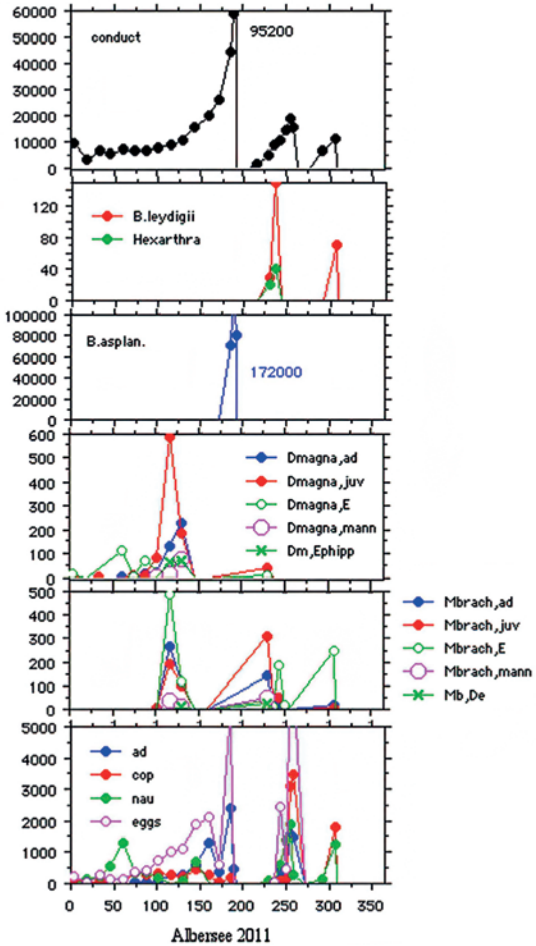

Fig. 5: Albersee 2011. Conduct: electric conductivity (µS.cm^{-1}); B. leydigii: *Brachionus leydigii* (ind.L^{-1}), Hexarthra: *Hexarthra* sp. (ind.L^{-1}); B. asplan: *Brachionus asplanchnoidis* (ind.L^{-1}); Dmagna: *Daphnia magna,* ad: adults (ind.L^{-1}), juv: juveniles (ind.L^{-1}), E: eggs.L^{-1}, mann: male (ind.L^{-1}), Ephipp: ephippia.L^{-1}; Mbrach: *Moina brachiata,* ad: adults (ind.L^{-1}), juv: juveniles (ind.L^{-1}), E: eggs.L^{-1}, mann: male (ind.L^{-1}), De: ephippia.L^{-1}; *Arctodiaptomus spinosus*, ad: adults (ind.L^{-1}), cop: copepodides (ind.L^{-1}), nau: nauplii (ind.L^{-1}), eggs: eggs.L^{-1}. – Abb. 5: Albersee 2011. Conduct: Leitfähigkeit (µS.cm^{-1}); B. leydigii: *Brachionus leydigii* (ind.L^{-1}), Hexarthra: *Hexarthra* sp. (ind.L^{-1}); B. asplan: *Brachionus asplanchnoidis* (ind.L^{-1}); Dmagna: *Daphnia magna,* ad: Adulte (ind.L^{-1}), juv: Juvenes (ind.L^{-1}), E: Eier.L^{-1}, mann: Männchen (ind.L^{-1}), Ephipp: Ephippien.L^{-1}; Mbrach: *Moina brachiata,* ad: Adulte (ind.L^{-1}), juv: Juvenes (ind.L^{-1}), E: Eier.L^{-1}, mann: Männchen (ind.L^{-1}), De: Ephippien.L^{-1}; *Arctodiaptomus spinosus,* ad: Adulte (ind.L^{-1}), cop: Copepodid (ind.L^{-1}), nau: Nauplien (ind.L^{-1}), eggs: Eier.L^{-1}.

59 mS.cm^{-1} to 95,2 mS.cm^{-1} within the last 4 days resulted in high mortality of *B. asplanchnoidis*. The second drying up phase was less spectacular, the conductivity before dryness was at 19 mS.cm^{-1} (17,5 g.L^{-1}). Before the rapid drying *B. leydigii*, *Hexarthra* sp. and *M. brachiata* dominated the plankton, in the final week of the pan with water mainly adults and copepodides of *A. spinosus* were present. At the end of the third drying phase a conductivity of 11,4 mS.cm^{-1} (salinity: 9,8 g.L^{-1}) was reached. *Moina* juveniles and a few adults and nauplii and copepodides of *A. spinosus* formed the zooplankton with 3,1 × 10^3 ind.L^{-1}.

Three drying up phases occurred in 2012, the first one already in March. By end of March salts effloresced and were subject to wind transport. The highest conductivity measured was 15,2 mS.cm^{-1} (salinity: 13,6 g.L^{-1}), copepodides and nauplii of *A. spinosus* dominated the zooplankton, *B. asplanchnoidis* contributed 3 %. After a dry period of 41 days the pan got partly filled, the aquatic phase lasted just for 14 days. In this period mainly nauplii of *A. spinosus* (68 %), *M. brachiata* (15 %) and a few *B. leydigii* and *B. asplanchnoidis* (together 7 %) developed. After another dry period of 45 days the pan got filled for 38 days. The highest conductivity measured was 6,7 mS.cm^{-1}. First *M. brachiata* dominated (77 %), then rotifers, mainly *Hexarthra* sp. (73 %), and in the last phase all developmental stages of *A. spinosus* (87 %).

The year 2013 started with about 150 days of rather low conductivity (<5 $mS.cm^{-1}$). Within this period, from mid April to mid May, *D. magna* developed very well and reached a density of 225 $ind.L^{-1}$, which were 38 % of total zooplankton; the other 62 % were contributed by all developmental stages of *A. spinosus*. This development was followed by the first drying up phase, which ended at a conductivity of 52,5 $mS.cm^{-1}$ (61,2 $g.L^{-1}$) at the 24th July. From the beginning of July the conductivity increased by a daily rate of 2,35 $mS.cm^{-1}$ (salinity: 1,7 $g.L^{-1}$). During the last week of this phase *A. spinosus* reached a density of 1510 $ind.L^{-1}$ (= 95 % of the zooplankton), 54 % were adults; 5 % contributed *B. leydigii*. The second wet phase of the pan lasted from mid August to beginning of September, the drying up ended at a conductivity of 8,5 $mS.cm^{-1}$ (7,1 $g.L^{-1}$). This phase was characterized by *A. spinosus* with a density of 3055 $ind.L^{-1}$(= 70 % of total zooplankton), 60 % being contributed by adults and *M.brachiata* (27 %).

In 2014 one drying up phase was documented. Like in 2013, February until beginning of June conductivities <5 $mS.cm^{-1}$ were measured, and in this period *Moina* developed a maximum population density of 1167 $ind.L^{-1}$. During June, the pan dried up rapidly, conductivity increasing at a daily rate of 2,91 $mS.cm^{-1}$; the day before falling dry the conductivity was 59,5 $mS.cm^{-1}$, the day of last plankton samples 51,3 $mS.cm^{-1}$ were measured. At the beginning of the drying up *B. asplanchnoidis* and *B. leydigii* contributed 7–16 % to the total zooplankton numbers, the rest presented *A. spinosus*. End of June, in the final phase of the drying phase only *A. spinosus* was found and its concentration was enormous, $35,2 \times 10^3$ $ind.L^{-1}$, 88,4 % being adults, which resulted in a biomass of 193 $mgdw.L^{-1}$ (= second highest biomass measured for the seven pans in 5 years).

Oberer Stinkersee

No drying up phase was detected in 2010. In spring, mid April until end of May, *M. brachiata* was dominating (75–80 % of total zooplankton) at conductivities of 7–11 $mS.cm^{-1}$. Mid July until mid September conductivities were above 10 $mS.cm^{-1}$; two maxima showed up, on end of July, with 21,3 $mS.cm^{-1}$ (sal: 24,3 $g.L^{-1}$), a second, end of August, with 16,3 $mS.cm^{-1}$ (sal: 17,1 $g.L^{-1}$). At the time of the maximum conductivities *A. spinosus* was prevailing (93 % of total zooplankton) and mainly adults were present (70 % of *A. spinosus* population). In between these maximum values conductivity values dropped to 19,7 $mS.cm^{-1}$ and further to 12,5 $mS.cm^{-1}$ and in this period *B. asplanchnoidis* reached 51 %, and *Moina* 31 % of total zooplankton.

In spring 2011 conductivities varied between 5 and 12 $mS.cm^{-1}$. End of April/beginning of May *Moina* developed a high population density (1090 $ind.L^{-1}$; 30 % of total zooplankton). All developmental stages of *A. spinosus* were present at this time, reaching high densities in May (560–2120 $ind.L^{-1}$). The first drying up started end of June and ended mid July, the daily increase in conductivity was 1,93 $mS.cm^{-1}$, at the end a conductivity of 59 $mS.cm^{-1}$ (sal: 111,2 $g.L^{-1}$) was reached. Before the pan dried up completely *A. spinosus* disappeared. In the last two weeks of drying *B. asplanchnoidis* was the dominant species, reaching a density of $62,2 \times 10^3$ $ind.L^{-1}$ and representing 68,5–99,4 % of total zooplankton; some *Moina* did also occur. In the second drying up phase conductivities of 31,3 $mS.cm^{-1}$ and 29,6 $mS.cm^{-1}$ are reached. At the beginning of that phase *M. brachiata* developed a density of 670 $ind.L^{-1}$ (= 40 % of total zooplankton), then 400 to 500 *Hexarthra* sp., *B. leydigii* and *A. spinosus* per litre could be counted, but close to the highest conductivities *B. asplanchnoidis* represented 93–99 % (maximum $31,8 \times 10^3$ $ind.L^{-1}$) of total zooplankton.

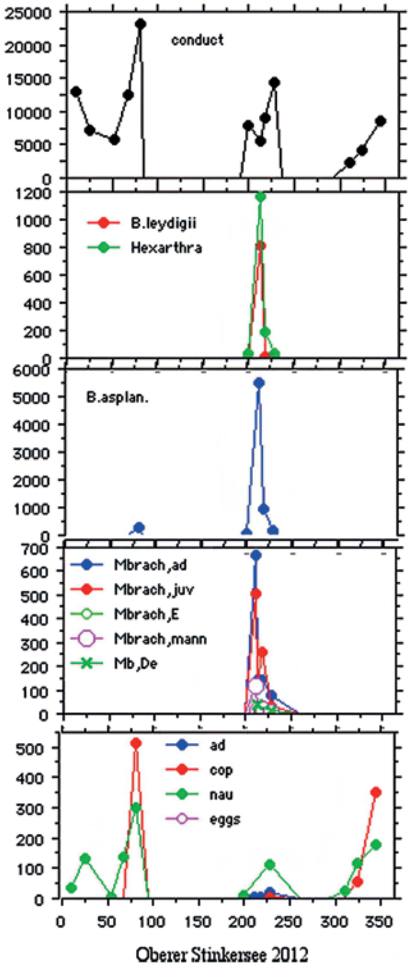

Fig. 6: Oberer Stinkersee 2012. Conduct: electric conductivity (µS.cm^{-1}); B. leydigii: *Brachionus leydigii* (ind.L^{-1}), Hexarthra: *Hexarthra* sp. (ind.L^{-1}); B. asplan: *Brachionus asplanchnoidis* (ind.L^{-1}); Mbrach: *Moina brachiata,* ad: adults (ind.L^{-1}), juv: juveniles (ind.L^{-1}), E: eggs.L^{-1}, mann: male (ind.L^{-1}), De: ephippia.L^{-1}; *Arctodiaptomus spinosus*, ad: adults (ind.L^{-1}), cop: copepodides (ind.L^{-1}), nau: nauplii (ind.L^{-1}), eggs: eggs.L^{-1}. – Abb. 6: Oberer Stinkersee 2012. Conduct: Leitfähigkeit (µS.cm^{-1}); B. leydigii: *Brachionus leydigii* (ind.L^{-1}), Hexarthra: *Hexarthra* sp. (ind.L^{-1}); B. asplan: *Brachionus asplanchnoidis* (ind.L^{-1}); Mbrach: *Moina brachiata,* ad: Adulte (ind.L^{-1}), juv: Juvenes (ind.L^{-1}), E: Eier.L^{-1}, mann: Männchen (ind.L^{-1}), De: Ephippien.L^{-1}; *Arctodiaptomus spinosus*, ad: Adulte (ind.L^{-1}), cop: Copepodid (ind.L^{-1}), nau: Nauplien (ind.L^{-1}), eggs: Eier.L^{-1}.

2012, after a dry winter, the drying up began already end of February and ended at the 25th of March at a conductivity of 23,1 mS.cm^{-1} (27,2 g.L^{-1}) (Fig. 6). At this time *B. asplanchnoidis* (290 ind.L^{-1}, 26 % of total zooplankton) and nauplii and copepodides (no adults) of *A.spinosus* (815 ind.L^{-1}, 74 %) represented the zooplankton. Then the pan was dry for 107 days. The second filling of the pan lasted for 36 days (July/August) and before falling again dry a conductivity of 14,4 mS.cm^{-1} (14,6 g.L^{-1}) was measured. *Moina* contributed up to 15 % of total zooplankton (1200 ind.L^{-1}) during this phase of drying up, but rotifers were the dominant zooplankters (43–99 % of total zooplankton), mainly *B. asplanchnoidis* (5500 ind.L^{-1}), *Hexarthra* sp. (1170 ind.L^{-1}) and *B. leydigii* (810 ind.L^{-1}). Then for 64 days the pan was dry and after the last filling just nauplii and copepodides of *A. spinosus* were present.

In spring 2013, mid March until mid May, the zooplankton was consisting first of nauplii and then of copepodides and adults of *A. spinosus*. At the beginning of the drying up phase (beginning of July), at conductivities between 12 and 25 mS.cm^{-1}, *B. leydigii* constituted 21 %, *A. spinosus* 34,4 % and *M. brachiata* 44,5 % of total zooplankton (2605 ind.L^{-1}). At conductivities between 25 mS.cm^{-1} and 56 mS.cm^{-1} (= conductivity before falling dry) (sal: 103,2 g.L^{-1}) the contribution of *B. asplanchnoidis* was 50–92 %, with maximum numbers in the final phase of drying of 5550 ind.L^{-1}. No individuals of *A. spinosus* survived until the end of this period.

In 2014 the pan dried up by mid June and reached a conductivity of 17,4 mS.cm^{-1} (18,6 g.L^{-1}). Before the drying started *M. brachiata* was dominating the zooplankton with a population density of 1890 ind.L^{-1} (= 82,4 % of total zooplankton). In the last phase of the drying up, end of May/beginning of June, *Moina* represented 55 %, all developmental stages of

A. spinosus 40 % (45 % of the *Arctodiaptomus* population were adults) and *B. leydigii* 5 %; the total zooplankton numbers were 2040 ind.L^{-1}.

Runde Lacke

2010 no drying up phase occurred, the conductivity varied between 7 and 9 mS.cm^{-1}, from mid July to end of September conductivity was above 10 mS.cm^{-1}, maxima measured were 15,8 mS.cm^{-1} (sal:14,2 g.L^{-1}) end of July and 14,6 mS.cm^{-1} (sal:13 g.L^{-1}) beginning of August. End of April/beginning of May *D. magna* was the dominant zooplankter (73,9 %; 1253 ind.L^{-1}). After the 20th of June *M. brachiata* (33,1 %; 385 ind.L^{-1}) and *A. spinosus* (51,5 %; 600 ind.L^{-1}) reached highest numbers. End of July the first phase of highest conductivities occurred, in this period the zooplankton consisted mainly of *B. leydigii* (94,5 %; 1190 ind.L^{-1}). End of August, the second phase of high conductivities, *B. asplanchnoidis* was most abundant (88,9 %; 4120 ind.L^{-1}), together with *B. leydigii* rotifers represented 97,9 % of total zooplankton. From mid-September until the end of the year the zooplankton consisted of *A. spinosus* with individual densities between 350 ind.L^{-1} and 935 ind.L^{-1}, representing about 95 % of total zooplankton throughout this time.

In 2011 Runde Lacke was not falling dry (Fig. 7). During spring conductivity measurements varied between 5 and 10 mS.cm^{-1}. In this period, beginning of May, *D. magna* represented 42,9 % of total zooplankton (130 ind.L^{-1}), *M. brachiata* and *A. spinosus* contributed 57,1 %. Between mid-June and mid-July conductivity increased to 21 mS.cm^{-1} (sal: 19,7 g.L^{-1}). At the beginning of this drying

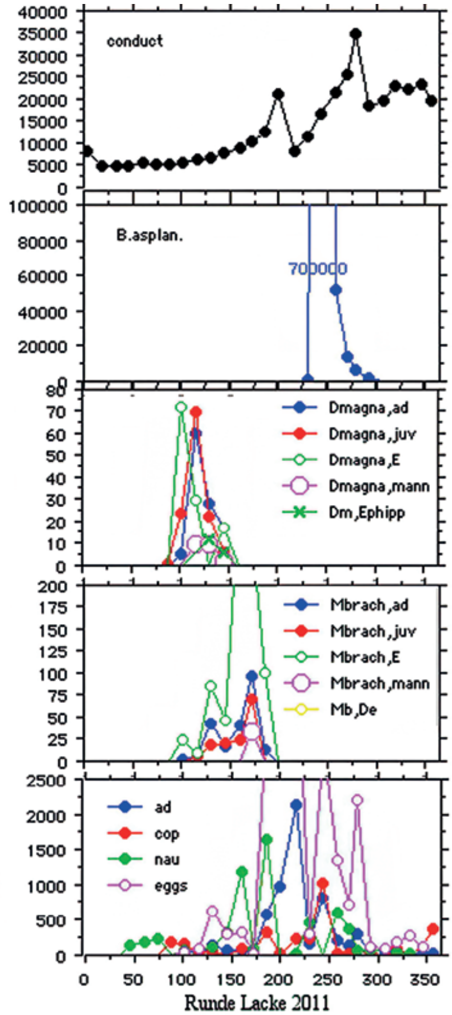

Fig. 7: Runde Lacke 2011. Conduct: electric conductivity (µS.cm^{-1}); B. asplan: *Brachionus asplanchnoidis* (ind.L^{-1}); Dmagna: *Daphnia magna,* ad: adults (ind.L^{-1}), juv: juveniles (ind.L^{-1}), E: eggs.L^{-1}, mann: male (ind.L^{-1}), Ephipp: ephippia.L^{-1}; Mbrach: *Moina brachiata,* ad: adults (ind.L^{-1}), juv: juveniles (ind.L^{-1}), E: eggs.L^{-1}, mann: male (ind.L^{-1}), De: ephippia.L^{-1}; *Arctodiaptomus spinosus*, ad: adults (ind.L^{-1}), cop: copepodides (ind.L^{-1}), nau: nauplii (ind.L^{-1}), eggs: eggs.L^{-1}. – Abb. 7: Runde Lacke 2011. Conduct: Leitfähigkeit (µS.cm^{-1}); B. asplan: *Brachionus asplanchnoidis* (ind.L^{-1}); Dmagna: *Daphnia magna,* ad: Adulte (ind.L^{-1}), juv: Juvenes (ind.L^{-1}), E: Eier.L^{-1}, mann: Männchen (ind.L^{-1}), Ephipp: Ephippien.L^{-1}; Mbrach: *Moina brachiata,* ad: Adulte (ind.L^{-1}), juv: Juvenes (ind.L^{-1}), E: Eier.L^{-1}, mann: Männchen (ind.L^{-1}), De: Ephippien.L^{-1}; *Arctodiaptomus spinosus*, ad: Adulte (ind.L^{-1}), cop: Copepodid (ind.L^{-1}), nau: Nauplien (ind.L^{-1}), eggs: Eier.L^{-1}.

period 31,7 % of total zooplankton were contributed by *M. brachiata*. This was followed by the rapid development of *A. spinosus* (2390 ind.L^{-1}; 98,8 % of total zooplankton), 88,7 % being adult specimens. The second phase of increasing conductivity, with the maximum of 34,7 mS.cm^{-1} (sal: 36 g.L^{-1}), was dominated by *B. aslplanchnoidis*, with the highest individual population density recorded so far, 669,4 × 10^{3}.L^{-1}. In September and October *B. asplanchnoidis* represented 93–99,7 % of total zooplankton. November and December conductivities varied between 20 and 25 mS.cm^{-1}, and all developmental stages of *A. spinosus* represented the zooplankton.

In 2012 the pan dried up twice; the first drying phase occured in April with a maximum conductivity of 39,1 mS.cm^{-1} (sal: 41,8 g.L^{-1}). This period was characterized by a rapid development of *B. asplanchnoidis* coming up to a population density of 3330 ind.L^{-1} (97,6 % of total zooplankton). *A. spinosus* also occurred, before the pan was drying up just adults did show up. After a dry phase of 80 days the pan got refilled and in August the next drying phase began. The highest conductivity during this time was 20,5 mS.cm^{-1} (sal: 19,1 g.L^{-1}). At the beginning of this drying phase again *B. asplanchnoidis* was the dominant species (79,6 %; 15,6 × 10^{3}.L^{-1}), *B. leydigii* and *Hexarthra* sp. contributed together 18.1 % (3,54 × 10^{3} ind.L^{-1}). At the time of highest conductivity *M. brachiata* (55,3 %; 470 ind.L^{-1}) and all developmental stages of *A. spinosus* (35,3 %; 300 ind.L^{-1}) were the prevailing zooplankton organisms. After 50 days without any water in the pan it got refilled, a new generation of *A. spinosus* developed.

Until beginning of July 2013 the conductivities measured varied between 2,7 mS.cm^{-1} and 7,1 mS.cm^{-1}. In March/April the zooplankton was dominated by *A. spinosus*. Beginning of May *D. magna* represented 42,2 % of total zooplankton (580 ind.L^{-1}). Beginning of July, the drying up phase started and the conductivity increased by a daily rate of 2,65 mS.cm^{-1}, ending at a maximum of 53,7 mS.cm^{-1} (sal: 63 g.L^{-1}). During this phase, first some *M. brachiata* developed (10,8 % of total zooplankton), then *B. leydigii* was dominant (5250 ind.L^{-1}; 92,6 %), and in the final phase of drying *B. asplanchnoidis* remained as the only plankton organism (8000 ind.L^{-1}; 100 %).

A very similar situation turned up in 2014. Early spring, conductivity values varied between 5 and 7 mS.cm^{-1}, *A. spinosus* was prevailing, end of April *D. magna* represented 23 % of the zooplankton, last week of May *M. brachiata* was quite numerous (385 ind.L^{-1}; 45,1 %) and at the beginning of the drying up phase *A. spinosus* was dominant (615 ind.L^{-1}; 73,2 %), 79,7 % of *A. spinosus* numbers being adults. During the last week of drying, the highest conductivity was 39,2 mS.cm^{-1} (sal: 42 g.L^{-1}), *B. leydigii* was the dominant zooplankton organism (2790 ind.L^{-1}; 90,5 %), together with some *B. asplanchnoidis* rotifers represented 98,9 % of total zooplankton.

Obere Hölllacke

Throughout 2010 this pan did not fall dry. During springtime, in May, conductivity varied between 8 mS.cm^{-1} and 11 mS.cm^{-1} and *M. brachiata* represented 42,9 %–69,2 % of total zooplankton; the highest population density was 1700 ind.L^{-1}. From beginning of July until mid-September conductivity increased from 10 mS.cm^{-1} to 18,4 mS.cm^{-1} (sal: 20 g.L^{-1}). At the time of highest conductivities *A. spinosus* was dominating (84,8–98,2 % of total zooplankton; 1845–4400 ind.L^{-1}), by mid-September *B. asplanchnoidis* represented 34,7–40,3 % of total zooplankton (1560–2010 ind.L^{-1}). The end of the year was dominated by all developmental stages of *A. spinosus*.

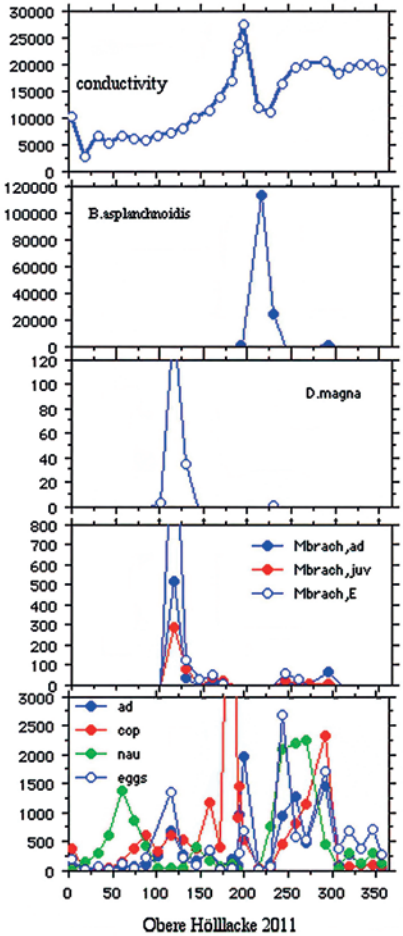

Fig. 8: Obere Hölllacke 2011. Conduct: electric conductivity (µS.cm^{-1}); B. asplan: *Brachionus asplanchnoidis* (ind.L^{-1}); Dmagna: *Daphnia magna* (total numbers.L^{-1}); Mbrach: *Moina brachiata,* ad: adults (ind.L^{-1}), juv: juveniles (ind.L^{-1}), E: eggs.L^{-1}; *Arctodiaptomus spinosus*, ad: adults (ind.L^{-1}), cop: copepodides (ind.L^{-1}), nau: nauplii (ind.L^{-1}), eggs: eggs.L^{-1}. – Abb. 8: Obere Hölllacke 2011. Conduct: Leitfähigkeit (µS.cm^{-1}); B. asplan: *Brachionus asplanchnoidis* (ind.L^{-1}); Dmagna: *Daphnia magna* (total numbers.L^{-1}); Mbrach: *Moina brachiata,* ad: Adulte (ind.L^{-1}), juv: Juvenes (ind.L^{-1}), E: Eier.L^{-1}; *Arctodiaptomus spinosus*, ad: Adulte (ind.L^{-1}), cop: Copepodid (ind.L^{-1}), nau: Nauplien (ind.L^{-1}), eggs: Eier.L^{-1}.

2011 Obere Hölllacke did not dry up completely (Fig. 8). Spring conductivities varied between 6 and 10 mS.cm^{-1}, *D. magna* (6,3 %), *M. brachiata* (34,2 %) and *A. spinosus* (58,2 %) contributed to total zooplankton numbers (2370 ind.L^{-1}). End of June and July revealed the highest conductivities, 13,8–27,5 mS.cm^{-1} (sal: 34,7 g.L^{-1}). The week before the highest conductivity was reached, *A. spinosus* dominated the zooplankton (62,7–96,9 %) with densities between 1060 and 2520 ind.L^{-1}, at the time of highest conductivity adults represented 78,2 % of the copepod density. This development of *A. spinosus* was followed by one of *B. asplanchnoidis* at the beginning of August, with a maximum density of 112,8 × 10^{3}.L^{-1} (100 % of zooplankton). The autumn was again dominated by *A. spinosus* at conductivities between 16 and 20 mS.cm^{-1}.

The year 2012 had two drying up phases, the first beginning in March and ending by mid-May, the highest conductivity was 26,7 mS.cm^{-1} (sal: 33,3 g.L^{-1}). The period of mid-April until complete drying up was dominated by rotifers (94,4–99,2 % of total zooplankton), *B. asplanchnoidis* represented 95 %, reached a density of 6670 ind.L^{-1} and *B. leydigii* contributed 180–550 ind.L^{-1} to the zooplankton. After a dry phase of 53 days, the pan was filled with water for 36 days, conductivity quickly raised to 9,3–11,4 mS.cm^{-1} and at the beginning of this phase the zooplankton consisted of rotifers (4160 ind.L^{-1}; 98,6 %), *B. asplanchnoidis* contributing 83,3 % and *B. leydigii* 13 %. At the end of this period *M. brachiata* represented 62 % of total zooplankton (310 ind.L^{-1}).

Obere Hölllacke did not dry up completely in 2013, but showed a drying phase with a daily increase in conductivity of 1,95 mS.cm^{-1} and a maximum conductivity of 48,6 mS.cm^{-1} (sal: 81,5 g.L^{-1}). A week before the highest conductivity, *A. spinosus* was the dominant zooplankton organism (6730 ind.L^{-1}), 30 % of the population were adults, at the time of the highest conductivity *B. asplanchnoidis* was dominant (90 % of total zooplankton; 810 ind.L^{-1}), some *B. leydigii* also contributed to the zooplankton standing stock.

In 2014, the drying up phase happened between mid-June and mid-July with a final conductivity of 38,1 mS.cm^{-1} (sal: 56 g.L^{-1}). Before the drying phase *M. brachiata* was prevailing, reached a maximum density of 1930 ind.L^{-1} (76,6 % of total zooplankton). At the beginning of the drying phase *A. spinosus* was dominant, but the higher the conductivity, the higher the contribution of the rotifers with *B. asplanchnoidis* contributing 77,6 % and *B. leydigii* 12,1 %.

Obere Halbjochlacke

During 2010 this pan was not completely falling dry. April/May conductivity values varied between 4 and 9 mS.cm^{-1}; the zooplankton consisted of *M. brachiata* with maximum numbers of 460 ind.L^{-1} and *A. spinosus* with highest numbers of 595 ind.L^{-1}. From end of July until end of August highest conductivities were measured (14–18,7 mS.cm^{-1}) and the zooplankton consisted of rotifers (58,7–92,2 %). At the beginning of this period *B. leydigii* contributed 42,8 % (1243 ind.L^{-1}) and *A. spinosus* 19,5 % (565 ind.L^{-1}; 81 % adult), at the time of the highest conductivity *B. asplanchnoidis* was dominating with maximum numbers of 5940 ind.L^{-1} (= 81,4 % of total zooplankton). In autumn conductivities varied between 5 mS.cm^{-1} and 9 mS.cm^{-1}, *A. spinosus* (all developmental stages) represented 52–72 % of total zooplankton numbers.

2011 three drying phases developed, the conductivities reached were 32,9 mS.cm^{-1} (sal: 45 g.L^{-1}), 33,8 mS.cm^{-1} (sal: 46,8 g.L^{-1}) and 27,1 mS.cm^{-1}(sal: 34 g.L^{-1}), rain in between the maxima diluted the water. End of April, before the first drying phase began, *D. magna* reached a density of 160 ind.L^{-1} (10,7 % of total zooplankton). At the beginning of the first drying phase, end of June, (conductivities >10 mS.cm^{-1}) *M. brachiata* was prevailing in the zooplankton (1030 ind.L^{-1}; 62,6 % of total zooplankton). When the highest conductivity was reached (32,9 mS.cm^{-1}), *A. spinosus* was the dominant plankter (89,5 %) with 2730 ind.L^{-1}, of which 85,3 % were adults.

At beginning September, the second drying phase started and *M. brachiata* developed a second peak (320 ind.L^{-1}; 21,8 %). At the time of highest conductivity, 33,8 mS.cm^{-1}, *B. asplanchnoidis* reached a density of 7300 ind.L^{-1} (= 99,8 % of zooplankton). During the last drying period (mid October – mid November) conductivity raised to 27,1 mS.cm^{-1}, the zooplankton consisted of nauplii and copepodides of *A. spinosus* (99,5 %) with a density of 6350 ind.L^{-1}.

Until end of December 2011 the pan was dry. Beginning of January 2012, the deepest part got filled with water and *A. spinosus* nauplii hatched out of resting eggs, the maximum numbers were 4330 ind.L^{-1}. No copepodids and adults did develop. The pan dried up by mid–March, having reached a conductivity of 9,4 mS.cm^{-1}. For 117 days the pan was dry and then partly filled from mid-July until mid-August. By end of July rotifers (*B. asplanchnoidis* and *B. leydigii*) reached maximum numbers of 630 ind.L^{-1} (55,4 % of total zooplankton) and *M. brachiata* numbers of 95–195 ind.L^{-1} (8,5–29,2 % of total zooplankton). During the first half of August a conductivity of 8,6 mS.cm^{-1} was measured, all developmental stages of *A. spinosus* were present and reached 1430 ind.L^{-1} (89,6 % of total numbers). After 61 days of dryness the pan filled again and nauplii and copepodides of *A. spinosus* developed.

2013 one drying up phase occurred between the 08th of July and 08th of August, with a final conductivity of 49,8 mS.cm^{-1} (84,7 g.L^{-1}), the last week before complete dryness the daily increase in conductivity was 5,2 mS.cm^{-1}. In July, at a conductivity of about 10 mS.cm^{-1} *M. brachiata* represented 55,5 % of total zooplankton and occurred at a density of 156 ind.L^{-1}. A week before complete dryness *A. spinosus* reached concentrations of 4970 ind.L^{-1} (= 97,1 % of total zooplankton), 47 % of the organisms being adults, the rest copepodides. During the last week, when conductivity increased to 49,8 mS.cm^{-1}, numbers of *A. spinosus* decreased, the survivors were mainly adults (82,8 %).

The situation in 2014 was comparable to 2013, with *M. brachiata* and *A. spinosus* being the dominant organisms. The drying up phase occurred already between end of May and mid-June and the conductivity attained was much lower, 11,9 mS.cm^{-1}, than in 2013. At the end of the drying phase the zooplankton consisted of 2595 ind.L^{-1}, *Moina* representing 49,7 % and *Arctodiaptomus* 48,7 %. In both populations the adults were prevailing (*Moina* – 58,1 %; *Arctodiaptomus* – 75,9 %).

Illmitzer Zicksee

In 2010 and 2011 this pan did not dry up (Fig. 9). As no sufficient data were available for 2010 the phenology of the year is not described. From March until mid-July of 2011 conductivity was steadily increasing from about 3 mS.cm^{-1} to 10,9 mS.cm^{-1}, and from beginning of August until reaching the highest conductivity of 15,4 mS.cm^{-1} (sal: 13,8 g.L^{-1}) beginning of October. Mid-April – mid-May *D. magna* developed at conductivities of 3,8–4,2 mS.cm^{-1} to a density of 210 ind.L^{-1} (32,5 % of total zooplankton). Mid-June – beginning of August, at conductivities of 6,5–10,9 mS.cm^{-1}, *A. spinosus* was dominant, represented on average 97,3 % of the zooplankton and reached a maximum

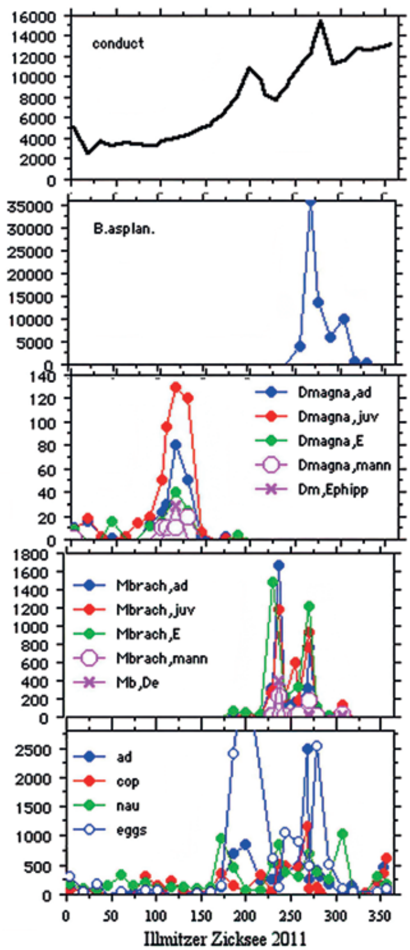

Fig. 9: Illmitzer Zicksee 2011. Conduct: electric conductivity (µS.cm^{-1}); B. asplan: *Brachionus asplanchnoidis* (ind.L^{-1}); Dmagna: *Daphnia magna,* ad: adults (ind.L^{-1}), juv: juveniles (ind.L^{-1}), E: eggs.L^{-1}, mann: male (ind.L^{-1}), Ephipp: ephippia.L^{-1}; Mbrach: *Moina brachiata,* ad: adults (ind.L^{-1}), juv: juveniles (ind.L^{-1}), E: eggs.L^{-1}, mann: male (ind.L^{-1}), De: ephippia.L^{-1}; *Arctodiaptomus spinosus*, ad: adults (ind.L^{-1}), cop: copepodides (ind.L^{-1}), nau: nauplii (ind.L^{-1}), eggs: eggs.L^{-1}. – Abb. 9: Illmitzer Zicksee 2011. Conduct: Leitfähigkeit (µS.cm^{-1}); B. asplan: *Brachionus asplanchnoidis* (ind.L^{-1}); Dmagna: *Daphnia magna,* ad: Adulte (ind.L^{-1}), juv: Juvenes (ind.L^{-1}), E: Eier.L^{-1}, mann: Männchen (ind.L^{-1}), Ephipp: Ephippien.L^{-1}; Mbrach: *Moina brachiata,* ad: Adulte (ind.L^{-1}), juv: Juvenes (ind.L^{-1}), E: Eier.L^{-1}, mann: Männchen (ind.L^{-1}), De: Ephippien.L^{-1}; *Arctodiaptomus spinosus*, ad: Adulte (ind.L^{-1}), cop: Copepodid (ind.L^{-1}), nau: Nauplien (ind.L^{-1}), eggs: Eier.L^{-1}.

density of 1470 ind.L^{-1}. Then, mid-August until the end of August, at conductivities between 7,7 and 9,1 mS.cm^{-1}, a first peak of *M. brachiata* showed up with a maximum density of 2860 ind.L^{-1} (58,4 % adults; 62,7 % of total zooplankton). A second peak of *Moina* (1700 ind.L^{-1}) appeared at the time of conductivities between 11,3–15,4 mS.cm^{-1}, at the same time *A. spinosus* adults developed high numbers (2500 ind.L^{-1}). But the dominant organism at the highest conductivities (maximum: 15,4 mS.cm^{-1}) was *B. asplanchnoidis*; the rotifer represented 71,5–92,9 % of total zooplankton and reached $35{,}9 \times 10^3$ ind.L^{-1}.

Two drying up phases occurred in 2012. The first one lasted from mid-April to mid-May and ended with a conductivity of 39,2 mS.cm^{-1} (sal: 42 g.L^{-1}). At the beginning of this phase, at conductivities between 15 mS.cm^{-1} and 35 mS.cm^{-1}, *B. asplanchnoidis* was the dominant zooplankter, represented 42,2–98,1 % of total zooplankton and reached a density of 8790 ind.L^{-1}. At the end of this drying up *A. spinosus* prevailed (70,4 % of total zooplankton; 1470 ind.L^{-1}) and 98,2 % of the copepods were adults. The second phase of drying started like the first one with dominance of rotifers, *B. asplanchnoidis*, *B. leydigii* and some *Hexarthra* (65,4–96,7 % of total zooplankton; 9050 ind.L^{-1}). Then *M. brachiata* represented 22,7–44,4 % of the zooplankton (maximum density: 295 ind.L^{-1}). At the end of the drying up phase *A. spinosus* reached a density of 3050 ind.L^{-1} (86,4 %) and adults formed 72,4 % of the copepod population.

In 2013, the drying up phase began end of July and ended beginning of September. The highest conductivity reached was 14,2 mS.cm^{-1} (sal: 12,6 g.L^{-1}). During the first two weeks of the drying phase, at conductivities of 9,6–13,8 mS.cm^{-1}, *B. leydigii* dominated the zooplankton (5650 ind.L^{-1}; 95,1 % of total zooplankton). In the last phase, before drying up, rotifers reached a density of 9750 ind.L^{-1} (87,3 % of total zooplankton), *B. asplanchnoidis* contributing 3600 ind.L^{-1}, *B. leydigii* 2750 ind.L^{-1}, and *Hexarthra* sp. 3250 ind.L^{-1}. In addition, 1210 ind.L^{-1} of *Moina* (10,8 % of total zooplankton) and 210 ind.L^{-1} of *Arctodiaptomus* (1,9 %) completed the zooplankton standing stock.

Discussion

Limnological parameters

Beside the high temperatures during day time, the pans were characterized by a well expressed difference between day and night temperatures which may reach 10–19° C. Marchant & Williams (1977 c, in Hammer 1986) measured a temperature variation of 12° C to 39° C in a single day in shallow Lake Cundare. Boros et al. (2017) mentioned a difference between daily maximum and minimum temperature of 28° C for pans within the Carpathian Basin.

The oxygen saturations found in the present study compare very well with the results in Boros et al. (2014). Jenkin (1932) found oxygen saturation ranging from 18,2 % to 113 % in Lake Nakuru and 44 % to 104,8 % in one day at Lake Elmenteita. Ashton & Schoeman (1983) measured midday oxygen saturation in surface water of Pretoria Salt Pan 12–415 %, oxygen declined by 22:00 to the anoxic state.

Although the salt concentrations varied considerably during the period of investigation, the ionic proportions showed a remarkable constancy. Similar results are found by Langbein (1961; cited in Hammer 1986), by Williams & Buckney (1976), who studied five lakes in Victoria (Austrlia) over four years, or by Bayly (1969) who found remarkably constant ion proportions in Red Rock Tarn and Lake Werowrap (Australia). However, Williams & Buckney (1976) provided also examples for varying ionic proportions with changing salinities. Obviously, there is evidence for constancy and variability of ionic proportions when salinities are changing.

Data from this study compare very well with the data from more than 30 years ago (Metz & Forró 1989, Schall 1990) or the more recent studies by Wolfram et al. (2004) and Boros et al. (2014) which is an indication that the chemical character of the pans studied did not change throughout that long period of time.

The DOC data match with the data from the Hungarian pans (Boros et al. 2008 a, b), maxima above 200 $mg.L^{-1}$ and mean values of 40 $mg.L^{-1}$. DOC values from the large (315 km^2) subsaline Neusiedler See are much lower with a mean of 15,9 $mg.L^{-1}$ and a maximum of 23 $mg.L^{-1}$ (data from 2010, Herzig unpublished). According to Waiser & Robarts (2000) inland saline lakes in semiarid regions of the Canadian prairies contain some of the highest known concentrations of dissolved organic carbon (DOC). They found a seasonal mean of 35 $mg.L^{-1}$ in Redberry Lake, a lake with a salinity of 20,9 $g.L^{-1}$. In certain pans the concentration of DOC is above 200 $mg.L^{-1}$. The main source of dissolved humic material is represented by the aerobic decay of macrophytes (*Phragmites*) (Waiser & Robarts 2000).

In a recent paper Boros et al. (2020) demonstrate through a multi-site comparison, a multi-year seasonal monitoring, and a laboratory experiment that the dissolved organic matter content of the highest DOC concentration soda pans is primarily of groundwater and emergent macrophyte origin. They also present a global mean of DOC in inland waters with the outstanding value of 90 $mg.L^{-1}$ for soda pans and an extreme maximum of 988 $mg.L^{-1}$ measured in the Carpathian Basin.

In four of the seven pans studied the mean total phosphorus values were in the milligramme range (Tab. 2). The average P_{tot} for the investigation period varied between 0,12 mg $P_{tot}.L^{-1}$ (Unterer Stinkersee) and 2,36 mg $P_{tot}.L^{-1}$ (Oberer Stinkersee). The maxima measured reached 12,6 mg $P_{tot}.L^{-1}$ and 20 mg $P_{tot}.L^{-1}$ in Oberer Stinkersee. In Boros et al. (2013) a mean value of 6,6 mg $P_{tot}.L^{-1}$ and a maximum of 58,7 mg $P_{tot}.L^{-1}$ is presented for turbid salt pans, values which are higher than the measurements from the present study. The subsaline Neusiedler See, situated west of the investigation area, reached a maximum annual mean of 0,16 mg $P_{tot}.L^{-1}$ during the period of eutrophication, nowadays values are below 0,05 mg $P_{tot}.L^{-1}$ (Wolfram & Herzig 2013). According to Hutchinson (1937) high levels of phosphorus are characteristic for lakes in endorheic regions. Hammer (1986) presents data from selected athalassic saline lakes which reveal a range of 0,1 to 215 mg $P_{tot}.L^{-1}$. The data from the pans of the Carpathian Basin fall within this range (Boros et al. 2013). Shallow freshwater lakes with annual mean of 0,1 mg $P_{tot}.L^{-1}$ are classified as eutrophic (Vollenweider & Kerekes 1980). The saline pans of the Carpathian Basin can be classified as naturally highly eutrophic to polytrophic systems.

The mean Chla values for the seven pans ranged between 6.8 $\mu g.L^{-1}$ and 43.8 $\mu g.L^{-1}$,the maxima between 349 and 485.4 $\mu g.L^{-1}$. A range of Chlorophyll a values of 2–150 $\mu g.L^{-1}$ were mentioned for the pans within the Carpathian Basin, 70–100 % of the algae were classified as picoplankton (Vörös L., in Boros et al. 2013). For comparison, eutrophic, shallow freshwater lakes reveal Chla values of 25–30 $\mu g.L^{-1}$ (Vollenweider & Kerekes 1980).

Biomass

The biomass values found in the pans can be classified as very high, the maxima for the pans studied vary between 65,6 and 22,7 mgdw.L^{-1}; the mean biomass values were 6,7–3,4 mgdw.L^{-1} (winter results are not included). High biomass developed in spring and during the drying up of the pan. Two outstanding result were found: one in Runde Lacke, when at the beginning of September 2011 a dense „soup" of *B. asplanchnoidis* developed

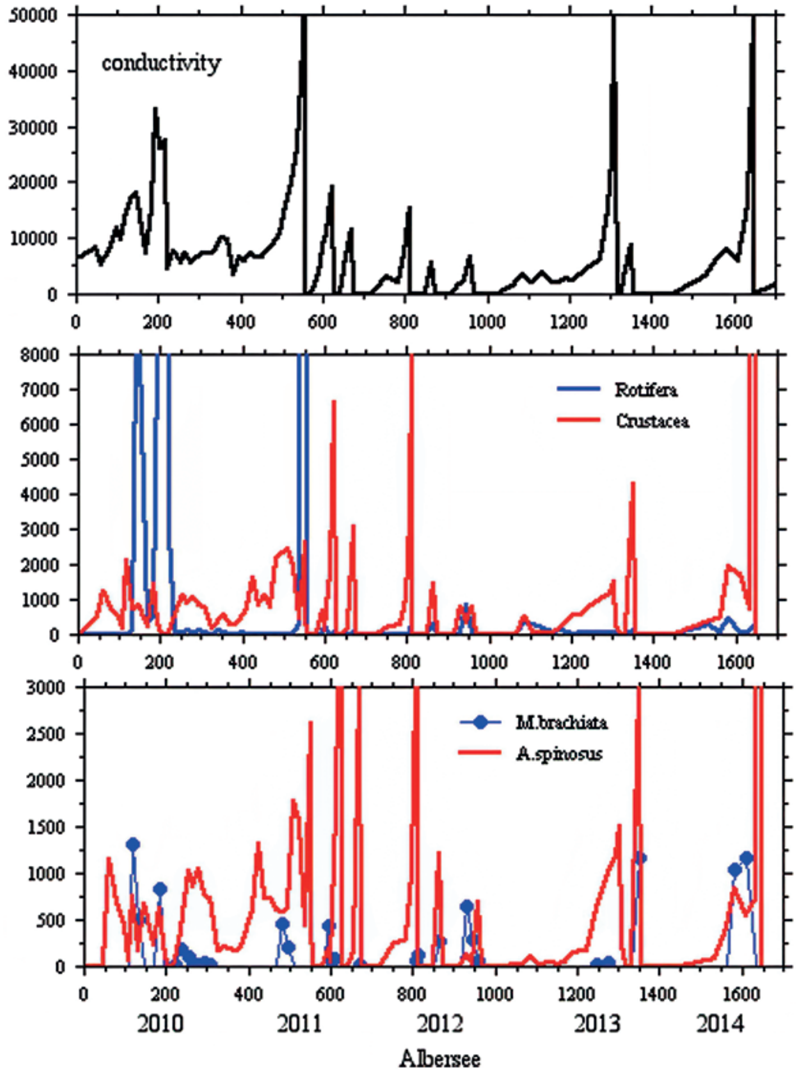

Fig. 10: Albersee 2010–2014. Conductivity: electric conductivity (µS.cm^{-1}); Rotifera, Crustacea (ind.L^{-1}); M.brachiata: *Moina brachiata* (ind.L^{-1}), A.spinosus: *Arctodiaptomus spinosus* (ind.L^{-1}). – Abb. 10: Albersee 2010–2014. Conductivity: Leitfähigkeit (µS.cm^{-1}); Rotifera, Crustacea (ind.L^{-1}); M.brachiata: *Moina brachiata* (ind.L^{-1}), A.spinosus: *Arctodiaptomus spinosus* (ind.L^{-1}).

(670.10^3 individuals.L^{-1}) forming a biomass of 298 mgdw.L^{-1} ; a second one, end of June, in the final phase of the drying up of Albersee only *A. spinosus* was found and its concentration was enormous, $35{,}2 \times 10^3$ ind.L^{-1}, 88,4 % being adults, which resulted in a biomass of 193 mgdw.L^{-1}.

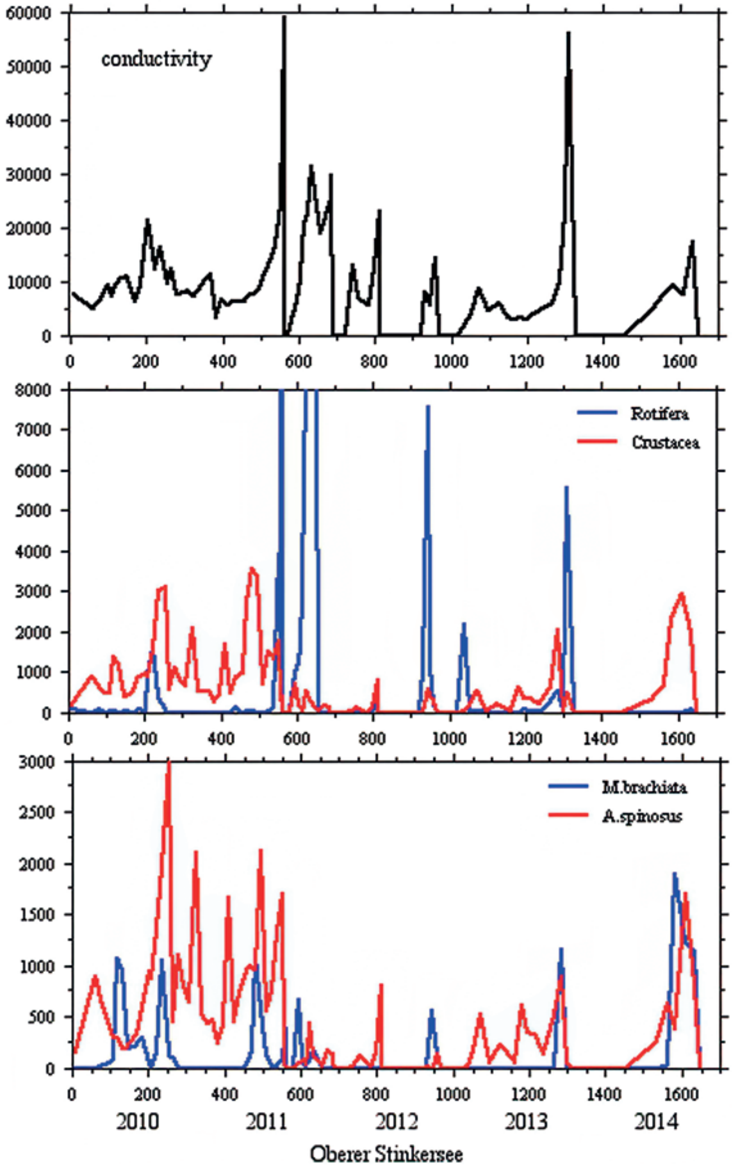

Fig. 11: Oberer Stinkersee 2010–2014. Conductivity: electric conductivity (µS.cm^{-1}); Rotifera, Crustacea (ind.L^{-1}); M.brachiata: *Moina brachiata* (ind.L^{-1}), A.spinosus: *Arctodiaptomus spinosus* (ind.L^{-1}). – Abb. 11: Oberer Stinkersee 2010–2014. Conductivity: Leitfähigkeit (µS.cm^{-1}); Rotifera, Crustacea (ind.L^{-1}); M.brachiata: *Moina brachiata* (ind.L^{-1}), A.spinosus: *Arctodiaptomus spinosus* (ind.L^{-1}).

These values compare very well with data from Hungarian salt lakes with maxima of 46,9 and 32,5 mgdw.L^{-1} and means (May–August) of 5,6 and 3,9 mgdw.L^{-1} (Boros et al. 2008 a). Similar values were found for rotifers in African soda lakes (max.: 620×10^3 individuals.L^{-1}; 52 mgdw.L^{-1}; Burian *et al.*, 2016). A comparison with zooplankton biomass from shallow freshwater lakes from temperate and tropical regions reveals the outstanding values from the soda pans. In shallow lakes of the temperate region (including eutrophic

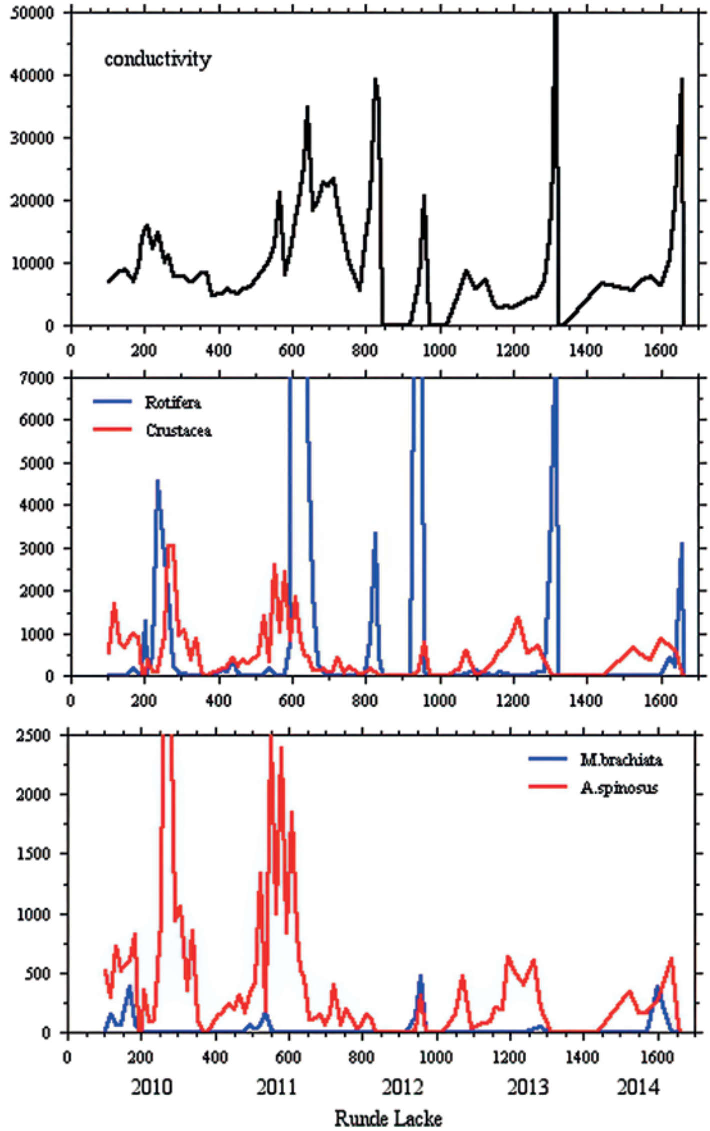

Fig. 12: Runde Lacke 2010–2014. Conductivity: electric conductivity (µS.cm^{-1}); Rotifera, Crustacea (ind.L^{-1}); M.brachiata: *Moina brachiata* (ind.L^{-1}), A.spinosus: *Arctodiaptomus spinosus* (ind.L^{-1}). – Abb. 12: Runde Lacke 2010–2014. Conductivity: Leitfähigkeit (µS.cm^{-1}); Rotifera, Crustacea (ind.L^{-1}); M.brachiata: *Moina brachiata* (ind.L^{-1}), A.spinosus: *Arctodiaptomus spinosus* (ind.L^{-1}).

systems) an annual mean of 0,5 mgdw.L^{-1} (e.g. Neusiedler See), in tropical Lake George 0,8 mgdw.L^{-1} is reached (Herzig, 2001). The recorded zooplankton biomass is less than 10 % of the values of the soda pans.

Such high zooplankton biomass offers an important food resource for several water birds (Winkler 1980, Horvath et al. 2012, 2013). A captive foraging experiment demonstrated that the filter-feeder wildfowl could successfully remove the microcrustacean plankton from the water (Boros et al. 2008 a). Northern Shoveler (*Spatula clypeata* (L.)) can also extract successfully rotifers (Euliss Jr. et al., 1997), zooplankton organisms that occur in the soda pans at very high concentrations.

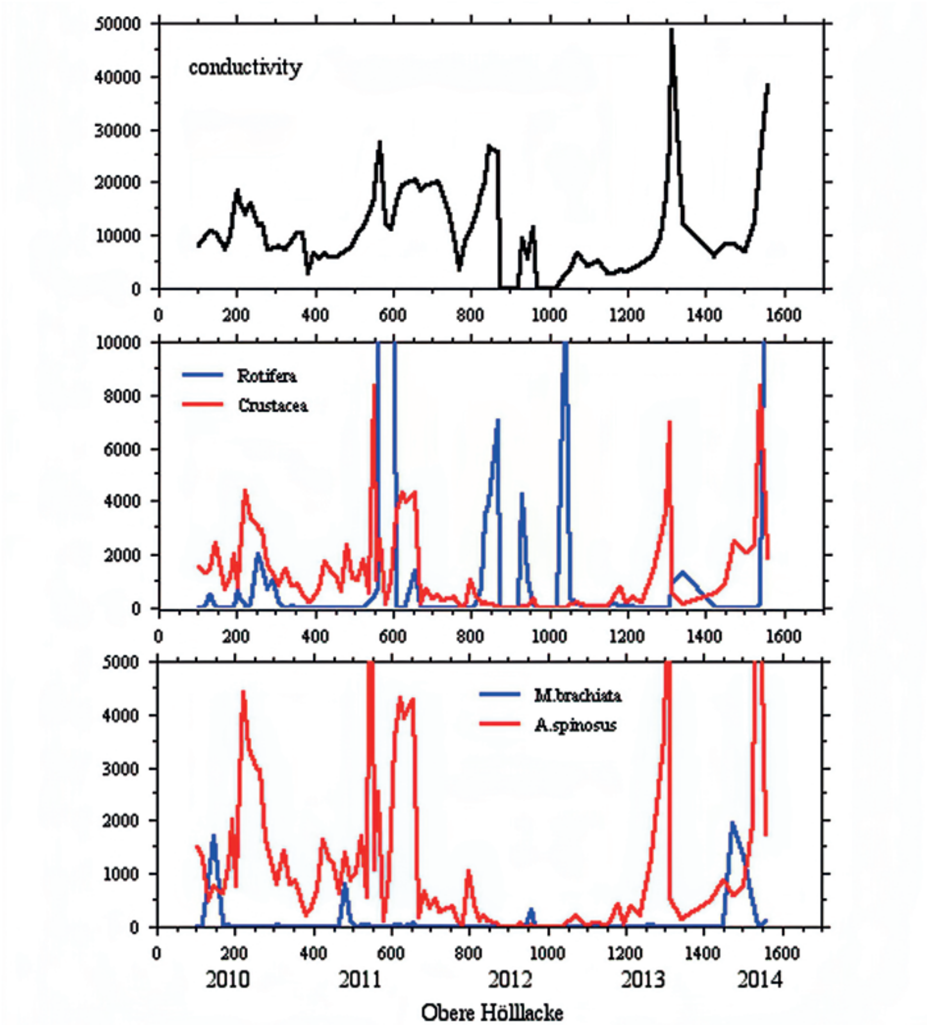

Fig. 13: Obere Hölllacke 2010–2014. Conductivity: electric conductivity (µS.cm^{-1}); Rotifera, Crustacea (ind.L^{-1}); M.brachiata: *Moina brachiata* (ind.L^{-1}), A.spinosus: *Arctodiaptomus spinosus* (ind.L^{-1}). – Abb. 13: Obere Hölllacke 2010–2014. Conductivity: Leitfähigkeit (µS.cm^{-1}); Rotifera, Crustacea (ind.L^{-1}); M.brachiata: *Moina brachiata* (ind.L^{-1}), A.spinosus: *Arctodiaptomus spinosus* (ind.L^{-1}).

Phenology of the drying up phase

The description of the phenologies of these phases of quick changes and rapid increase of conductivity and the obvious differences year to year, give an insight into the dynamics of these extreme waterbodies. It shows how rapid changes in the zooplankton community occur and how large the differences in population density develop within short time periods. This is summarized in Figures 10–15, which show conductivity and individuals.L^{-1}

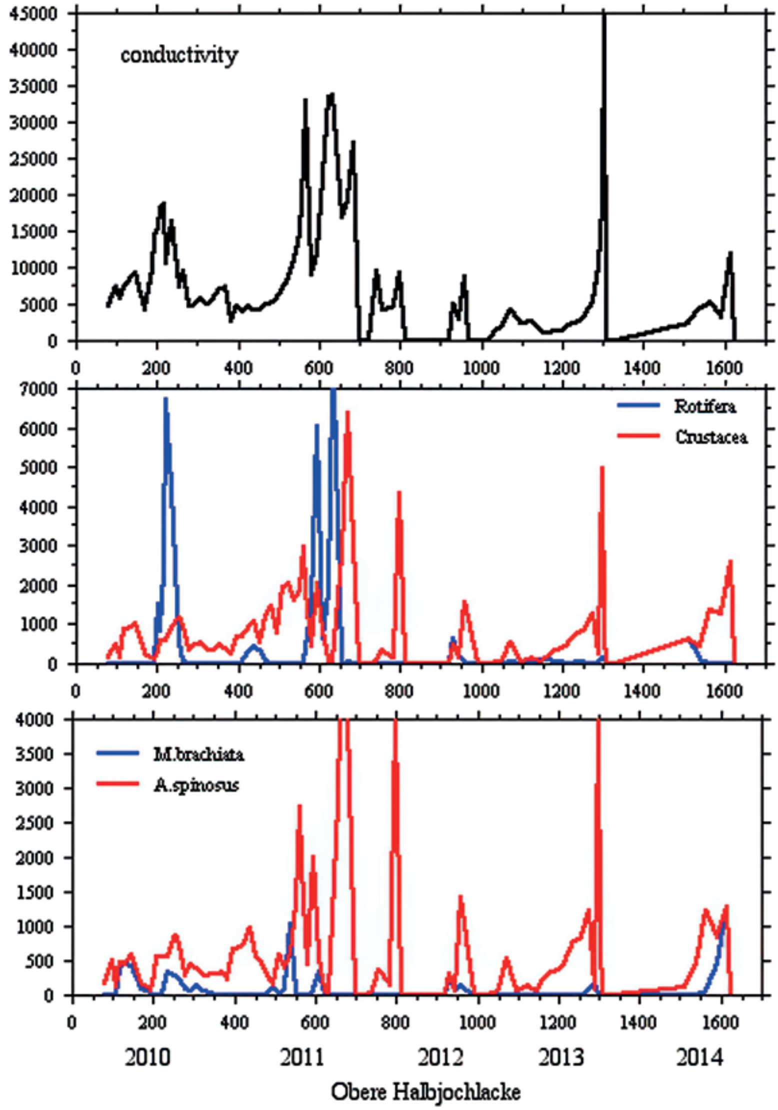

Fig. 14: Obere Halbjochlacke 2010–2014. Conductivity: electric conductivity (µS.cm^{-1}); Rotifera, Crustacea (ind.L^{-1}); M.brachiata: *Moina brachiata* (ind.L^{-1}), A.spinosus: *Arctodiaptomus spinosus* (ind.L^{-1}). – Abb. 14: Obere Halbjochlacke 2010–2014. Conductivity: Leitfähigkeit (µS.cm^{-1}); Rotifera, Crustacea (ind.L^{-1}); M.brachiata: *Moina brachiata* (ind.L^{-1}), A.spinosus: *Arctodiaptomus spinosus* (ind.L^{-1}).

(Rotifera, Crustacea, *Moina brachiata* and *Arctodiaptomus spinosus*) for Albersee, Illmitzer Zicksee, Runde Lacke, Oberer Stinkersee, Obere Hölllacke and Obere Halbjochlacke for the years 2010–2014.

The highest conductivity measured was for Albersee – 95,2 $mS.cm^{-1}$, followed by Oberer Stinkersee – 59 $mS.cm^{-1}$, Runde Lacke – 53,7 $mS.cm^{-1}$, Obere Halbjochlacke – 49,8 $mS.cm^{-1}$, Obere Hölllacke – 48,6 $mS.cm^{-1}$ and Illmitzer Zicksee – 39,2 $mS.cm^{-1}$. For compari-

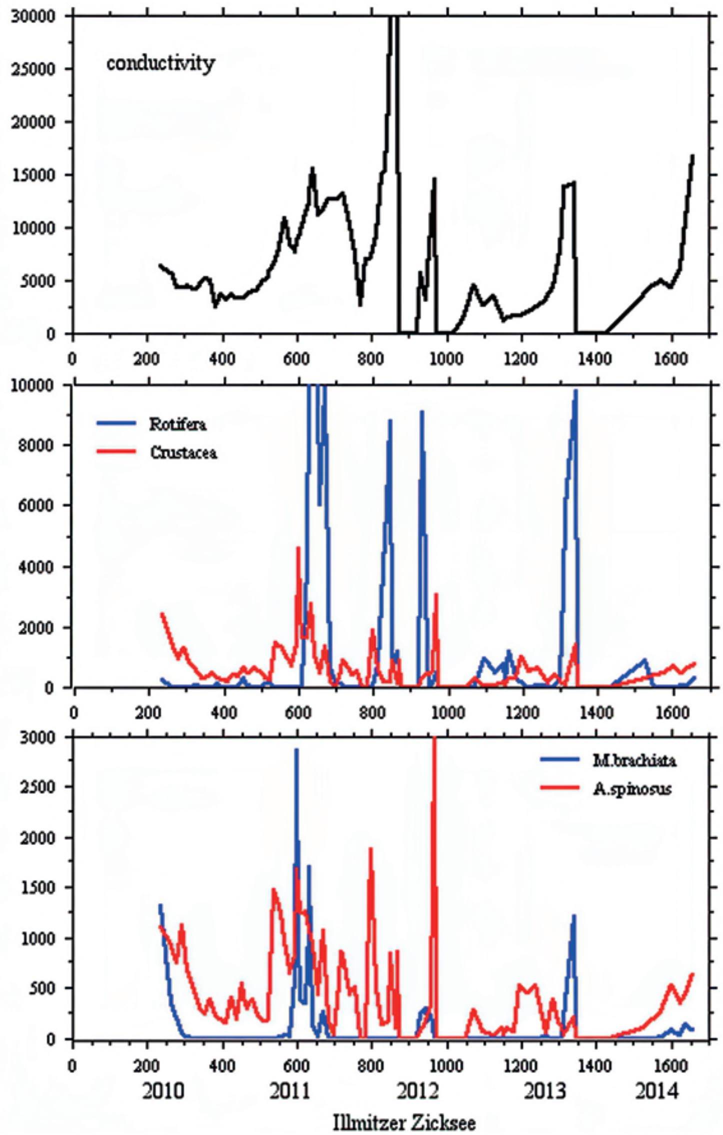

Fig. 15: Illmitzer Zicksee 2010–2014. Conductivity: electric conductivity ($\mu S.cm^{-1}$); Rotifera, Crustacea ($ind.L^{-1}$); M.brachiata: *Moina brachiata* ($ind.L^{-1}$), A.spinosus: *Arctodiaptomus spinosus* ($ind.L^{-1}$). – Abb. 15: Illmitzer Zicksee 2010–2014. Conductivity: Leitfähigkeit ($\mu S.cm^{-1}$); Rotifera, Crustacea ($ind.L^{-1}$); M.brachiata: *Moina brachiata* ($ind.L^{-1}$), A.spinosus: *Arctodiaptomus spinosus* ($ind.L^{-1}$).

son, Forró (1989) measured in the most sodic Szappanosszék (Fülöpháza pans) a maximum conductivity of 83,3 $mS.cm^{-1}$ in June.

In 74 % of all the drying and drying up phases rotifers dominated the zooplankton or, in many cases *B. asplanchnoidis* was the only plankton organism present. This is in contrary to findings in earlier studies on the soda pans (HORVATH et al. 2014, TOTH et al. 2014), which stated soda pans are mostly dominated by crustaceans rather than by rotifers, which could not become dominant in the pans. In all the other cases of drying up, *A. spinosus* was dominating, and at the very end of this phase mostly adults were abundant.

The highest individual densities of *B. asplanchnoidis* were 669×10^3 $ind.L^{-1}$ in Runde Lacke at a conductivity of 34,7 $mS.cm^{-1}$ and 204×10^3 $ind.L^{-1}$ at 33 $mS.cm^{-1}$ and 172×10^3 $ind.L^{-1}$ at 80 $mS.cm^{-1}$ in Albersee. Similar results are reported for the euryhaline *Brachionus dimidiatus* from Mare de Latir with a highest population density of 620×10^3 $ind.L^{-1}$ at 50 $mS.cm^{-1}$, from Lac de Liwa 365×10^3 $ind.L^{-1}$ at 25 $mS.cm^{-1}$ and from Lac de Bodou 236×10^3 $ind.L^{-1}$ at 40 $mS.cm^{-1}$ (ILTIS & RIOU-DUWAT 1971, cited in HAMMER 1986). The authors concluded that salinities above 70 $g.L^{-1}$ (above 73 $mS.cm^{-1}$) eliminated the rotifers from the temporary ponds each year.

B. asplanchnoidis is a strictly haline species (FONTANETO et al. 2006) and is found in the study by HORVATH et al. (2014) in the upper part of the conductivity gradient (20–50 $mS.cm^{-1}$). Following the results of the present study its first appearance in the pans is correlated with a conductivity >7 $mS.cm^{-1}$, the highest individual numbers are reached at a conductivity of 12–95 $mS.cm^{-1}$. Recent growth experiments demonstrated that *B. asplanchnoidis* shows positive population growth rates up to a conductivity of 50 $mS.cm^{-1}$, but experiments at 60 $mS.cm^{-1}$ revealed only negative growth rates (HERZIG unpublished results). This compares very well with the results reported for *B. dimidiatus* (see above) and it means that all the findings of *B. asplanchnoidis* in the field at higher conductivities just reflect short time survival but not successful population growth.

M. brachiata, the most prominent Cladocera in the pans studied, reached its population maxima of 1030–2360 $ind.L^{-1}$ at conductivities between 7,5 and 14,2 $mS.cm^{-1}$, the conductivities of its occurrence varied between 1 and 59 $mS.cm^{-1}$. According to METZ & FORRÓ (1991) it is confined to warmer periods, tolerates more saline waters and conductivities up to 35 $mS.cm^{-1}$. SCHALL (1990) found *Moina* in the same pans like in the present study at 1,6–46 $mS.cm^{-1}$. She also performed laboratory experiments on survival of these animals and found a seasonal change of the optimum salinity for their survival.

A. spinosus, a soda water specialist, is known as a highly tolerant calanoid copepod (METZ & FORRÓ 1991, HORVATH et al. 2014, TOTH et al. 2014,). It can be the dominant zooplankter in all pans at all seasons. It reached its maximum densities of 1600–8350 $ind.L^{-1}$ at conductivities varying between 8,5 and 48 $mS.cm^{-1}$. One outstanding density, 35200 $ind.L^{-1}$, was reached in Albersee at a conductivity of 51,3 $mS.cm^{-1}$; 88,4 % were adult specimens and they have been alive at this conductivity. At a conductivity of 59 $mS.cm^{-1}$ a high mortality was recognized. It seems, that its tolerance limit is around 50 $mS.cm^{-1}$. On the other hand its optimum for development is much lower. According to the experiments by NEWRKLA (1978) on development times of nauplii and copepodides and respiration rates, the optimum alkalinity is 100 $meq.L^{-1}$, salinity 12,6 $g.L^{-1}$ and conductivity 12,8 $mS.cm^{-1}$.

Unfortunately not more ecophysiological studies are available for these species, but they are urgently needed for further understanding of the processes in these salt pans.

Conclusion and conservation status

Salinity represents a major structuring gradient in aquatic systems. Inland saline lakes show a monotonous decline in diversity along increasing salinity. The most saline habitats have communities of one or two species only, with maximum densities well above 1000 ind.L^{-1}, up to 10^5 ind.L^{-1}.

Species in ephemeral lakes need to be adapted to large variability of salinity, temperature, oxygen and cyclical draughts of varying duration. As mentioned above, the ecophysiological information about the adaptation phenomena, as well as the genetic background are insufficient or missing.

Nevertheless, salt steppes and salt marshes, including the salt lakes, are unique habitats within Europe, they are listed as habitats of major importance in Appendix I of Directive 92/43 EEC on the conservation of natural habitats, Nr. 1530 „Pannonic salt steppes and salt marshes".

However, the conservation status of the soda pans is critical. From the beginning of the 20th century wide-spread artificial draining took place, which did withdraw the surface waters from the area very effectively and also lowered the water table in waterlogged soils. In addition, long-term extraction of groundwater for irrigation exceeded long-term recharge rates leading to regional groundwater overexploitation. This management resulted in a 75 % reduction of the water surface area by the end of the 20th century (Herzig 1994). A similar tendency was reported by Boros et al. (2013) for the soda pans from the Danube-Tisza Interfluve Region, they mention a decrease of 86 %.

Predictions concerning climatic changes in the Carpathian Basin warn about the increased occurrence of extreme climatic phenomena. Most of the climatic scenarios foresee milder and slightly wetter winters and dryer summers with more periods of droughts. As a consequence, climatic water deficiency is expected (Boros *et al.* 2013).

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