Spatio-temporal distribution of ostracod species in saline inland lakes (Mansfeld lake area; Central Germany)

Marlene Hoehle [Corresp., 1], **Claudia Wrozyna** [Corresp. 2]

[1] Institute for Geophysics and Geology, Universität Leipzig, Leipzig, Germany

[2] Institute for Geography and Geology, Universität Greifswald, Greifswald, Germany

Corresponding Authors: Marlene Hoehle, Claudia Wrozyna
Email address: marlene.hoehle@uni-leipzig.de, claudia.wrozyna@uni-greifswald.de

Ostracods are a diverse group of microcrustaceans with a ubiquitous distribution in a wide array of aquatic habitats and are common constituents of lake sediments. Inferences on temporal-spatial distribution of ostracod species is the prerequisite for reconstructions of palaeoenvironmental conditions. This requires a precise knowledge not only about ecological preferences and specific life histories, but also the understanding how (local) ecological parameters affect ostracod species assemblages (abundance and composition). Generally, these studies are rare and often characterized by an insufficient differentiation of living specimens from the total amount of valves of the modern population leading to uncertainties in species occurrences and diversity data. Modern ostracod populations were sampled from 12 water bodies within a relatively small study area (Mansfeld lake area, Central Germany). Physico-chemical parameters (temperature, oxygen content, conductivity, pH) were measured *in situ* and the uppermost 2 cm of sediment were collected in different seasons (April, June, September). Relative abundances of ostracods (living and dead), differentiated for adults and juveniles, were used for statistical analyses (Spearman`s rank correlation, Canonical correspondence analysis, Cluster analyses, Fisher´s α), to investigate relationships between species distribution and environmental factors as well as to identify habitat similarities and ostracod species assemblages. In total, 27 ostracod species (20 living species) were identified. Majority of them are considered as very common (cosmopolitan) freshwater species. Only two species are usually known from brackish water (*Cytheromorpha fuscata* and *Cyprideis torosa*). This is the first confirmation of living *C. torosa* in German inland waters. The relative abundances of ostracods show strong fluctuations during the study period and differences in composition of the ostracod species assemblages between and within the water bodies. There are also strong differences between bio- and taphocoenoses. The measured physico-chemical parameters which are usually considered as most important drivers on ostracod species distribution do not contribute to explain the observed temporal-spatial distribution

of the ostracod species. Differences in taphocoenoses show, that taphonomic processes can be very local and the sampling site, as well as the sampling time, is crucial. Biodiversity of ostracods is biased by sampling time, the variability of the ostracod assemblages between sampling month and the relationship between abundance of valves and living ostracods is not straightforward. Therefore, without precise knowledge of the ecological requirements of a species at a local scale, uncertainties may exist for the palaeoecological indication of a species.

Spatio-temporal distribution of ostracod species in saline inland lakes (Mansfeld lake area; Central Germany)

Marlene Hoehle[1], Claudia Wrozyna[2]

[1]Institute for Geophysics and Geology, University of Leipzig, Leipzig, Germany.
[2]Institute for Geography and Geology, University of Greifswald, Greifswald, Germany.

Corresponding Author:
Marlene Hoehle[1]
Talstraße 35, 04103 Leipzig, Germany
Email address: marlene.hoehle@uni-leipzig.de

Claudia Wrozyna[2]
Friedrich-Ludwig-Jahn-Str. 17a, 17489 Greifswald, Germany
Email address: claudia.wrozyna@uni-greifswald.de

Abstract

Ostracods are a diverse group of microcrustaceans with a ubiquitous distribution in a wide array of aquatic habitats and are common constituents of lake sediments. Inferences on temporal-spatial distribution of ostracod species is the prerequisite for reconstructions of palaeoenvironmental conditions. This requires a precise knowledge not only about ecological preferences and specific life histories, but also the understanding how (local) ecological parameters affect ostracod species assemblages (abundance and composition). Generally, these studies are rare and often characterized by an insufficient differentiation of living specimens from the total amount of valves of the modern population leading to uncertainties in species occurrences and diversity data.

Modern ostracod populations were sampled from 12 water bodies within a relatively small study area (Mansfeld lake area, Central Germany). Physico-chemical parameters (temperature, oxygen content, conductivity, pH) were measured *in situ* and the uppermost 2 cm of sediment were collected in different seasons (April, June, September). Relative abundances of ostracods (living and dead), differentiated for adults and juveniles, were used for statistical analyses (Spearman`s rank correlation, Canonical correspondence analysis, Cluster analyses, Fisher´s α), to investigate relationships between species distribution and environmental factors as well as to identify habitat similarities and ostracod species assemblages.

In total, 27 ostracod species (20 living species) were identified. Majority of them are considered as very common (cosmopolitan) freshwater species. Only two species are usually known from brackish water (*Cytheromorpha fuscata* and *Cyprideis torosa*). This is the first confirmation of living *C. torosa* in German inland waters. The relative abundances of ostracods show strong fluctuations during the study period and differences in composition of the ostracod species assemblages between and within the water bodies. There are also strong differences between bio- and taphocoenoses.

The measured physico-chemical parameters which are usually considered as most important drivers on ostracod species distribution do not contribute to explain the observed temporal-spatial distribution of the ostracod species. Differences in taphocoenoses show, that taphonomic processes can be very local and the sampling site, as well as the sampling time, is crucial.

Biodiversity of ostracods is biased by sampling time, the variability of the ostracod assemblages between sampling month and the relationship between abundance of valves and living ostracods is not straightforward. Therefore, without precise knowledge of the ecological requirements of a species at a local scale, uncertainties may exist for the palaeoecological indication of a species.

1. Introduction

Despite their high diversity, vast array of ecosystem services, basic science on invertebrates is scarce and underfunded which contributes to that most species remain undescribed. Scarce population time series of invertebrates contribute to poor knowledge of the spatial and temporal distribution of species as well as their ecological preferences is mostly unknown (Baillie et al., 2008; Cardoso et al., 2011; Outhwaite et al., 2020).

Ostracods (bivalved microcrustaceans), are one of the most diverse groups of living benthic invertebrates (Horne et al., 2019), inhabit almost all types of aquatic environments: marine, freshwater and even some semi-terrestrial (Horne et al., 2002). In particular, freshwater ostracods are of great interest in a variety of ecological and evolutionary studies because they are partially found *en masse* in aquatic environments and their calcified valves are common and well preserved in lake sediments (Martens et al., 2008) which enable to study long-term trends e.g., biodiversity. Although ostracods have generally very broad ecological tolerances, distribution is mainly determined by a variety of physico-chemical (abiotic) factors (temperature, pH, salinity, oxygen content, substrate type and depth) (Mezquita et al., 2005), as well as biotic factors (competition, predation, commensalism) (Guisan et al., 2010) and each species has specific tolerances and preferences to these factors (Kiss, 2007). Especially, temperature and salinity are considered as major controlling factors for distribution of freshwater ostracod species (Ruiz et al., 2013).

Precise autecological inferences based on fossil material depends on extensive knowledge about the ecological requirements and life-cycle information of the different species, as well as additionally (local) influences on these. Nonetheless, comprehensive studies on these are still rare (Külköylüoğlu et al., 2017; Viehberg, 2005). However, life cycle (or seasonal distribution),

97 ecology, and transfer into the geologic record (taphonomic processes) have rarely been
98 considered together. This, in turn, is problematic, as sometimes incorrect diversity estimates are
99 obtained and, most importantly, imprecise assumptions are made about ecological preferences or
100 (subtle) responses to environmental changes are overlooked, which leads to a discrepancy
101 between Recent and fossil data. Also problematic is the, often, insufficient differentiation
102 between living ostracods (biocoenoses) and valves (taphocoenoses). Diversity and autecology of
103 species are usually evaluated on the basis of Recent material (but usually only valves). Species or
104 entire assemblages may be, thus, assigned to incorrect environmental conditions. In addition,
105 studies are mostly based on large-scale trends, which are transferred to local scales (e.g., Pint *et*
106 *al.*, 2017).
107 The Mansfeld lake area provides within a narrow geographical area several water bodies
108 differing slightly with respect to hydrochemistry, hydro(geo)logy or degree of pollution settled.
109 These water bodies offer as `natural laboratories´ ideal conditions to study the effects of regional
110 and local environmental parameters and their seasonal fluctuations on the distribution of
111 individual ostracod species, but also on the entire community.
112 The main objective of this study is to characterize ostracod species in slightly saline inland
113 waters and their spatio-temporal distribution. For this purpose, the following research questions
114 were defined: (1) Are there disparities between the water bodies in terms of physico-chemical
115 characteristics and ostracod assemblages? (2) By repeated sampling in three months, can
116 differences in species abundance and richness of living ostracods be determined, which may
117 provide inferences about the species life cycle? (3) Can conclusions on taphonomic processes in
118 the waterbodies be drawn, by differentiating between living ostracods and valves? (4) Are

119 possible variations in living ostracod assemblages (abundance and richness) related to the
120 physico-chemical parameters of the water bodies?
121

122 **2. Materials and methods**

123 ***Study area***

124 The Mansfeld lake area is located 25 km west of Halle (Saale), a city of Saxony-Anhalt, in the
125 centre of the central German dry region (Fig 1). It is characterized by low precipitation (428
126 mm/a), a negative water balance, as well as short and pronounced extreme rainfall events
127 (Wennrich, 2005). The regional climate is characterised by a warm-toned mesoclimate, with
128 subcontinental tendencies and an annual mean temperature of 8.8°C (Trost and Rauchhaus, 2000;
129 Wennrich et al., 2005). Another peculiarity of the region is the natural salinity of the water
130 bodies, which is caused by saline inflows of salt deposits of Permian age from the underground
131 (Wennrich et al., 2007). Most of the investigated water bodies (KS, BS, TE, TE2, QW and MG)
132 lie within the area of the former lake `Salziger See´ (overview of the sampling localities and their
133 abbreviations are provided in Table 1). North of the former `Salziger See´is ` Süßer See´, which
134 is directly connected by ditches with KS, BS and MG. Both (`Süßer See´ and former `Salziger
135 See´) are located in the deepest part of a large depression (Teutschenthal Anticline) (Wennrich et
136 al., 2007). The remaining water bodies (OT, OT2, WL, TA, ST) are located outside this area,
137 topographically higher and with a maximum distance of 3 km, but mostly located at the marginal
138 area of the former `Salziger See´ (Fig 1). Although the water bodies presumably all have the
139 same catchment, they have different sub-catchments, and the water bodies outside the anticline
140 have different hydrological conditions (e.g., saline inflows) (John et al., 2000).
141

142 ***Sampling and data collection***

143 Three sampling campaigns were carried out in 2019 (April 16, June 7 and September 12) in the
144 Mansfeld lake area. During each sampling campaign, 10-12 water bodies (ponds, small lakes,
145 ditch) were investigated. An overview about the sampling localities is provided in Table 1.
146 Generally, we tried to visit the same sampling site at each water body during each campaign as
147 far as possible. Exceptions were made at the lakes TE and ST due to limited access due to dense
148 vegetation of the first sampling site. The sampling localities differed ~80 m north (TE) and
149 120 m east (ST), respectively, from the first site.
150 Physico-chemical variables (water temperature, electrical conductivity, pH and oxygen content)
151 were measured *in situ* using probes of the company WTW. Salinity was measured *in situ* as
152 electrical conductivity and converted (Rice et al., 2017) to salinity for direct comparison with
153 literature. All salinity values are in practical salinity units. Sediment samples were collected from
154 the uppermost few (approx.1-2) centimetres of sediment in the littoral zone using a hand net
155 within an area of ~1-2 m^2.
156 The samples were fixed with 70% Ethanol in the field at the time of collection, to preserve living
157 specimens. The sediment samples were washed with tap water through standard sieves sizes
158 (1000 µm, 500 µm, 250 µm and 125 µm). The sieve residues from mesh sizes 500 µm and 250
159 µm were transferred to sample bags using 70% ethanol, mesh size 125 µm were oven-dried. For
160 some water bodies, 125 µm fraction was considered on a trial basis, but not included in the study
161 due to the extremely small numbers of valves. Ostracods were separated from sediment and
162 species were sorted under a binocular microscope. Ostracods were assumed to have been alive
163 (biocoenoses) at the time of collection, when carapaces were slightly open and with intact and
164 well preserved soft parts. Valves and carapaces (empty or with soft part fragments) found, may

include not only dead individuals, but also those shed during moulting (juveniles) and are assumed as taphocoenoses. Due to the fact it is a natural assemblage, taphocoenoeses is probably a mix of thanatocoenoses and taphocoenoses (Boomer et al., 2003).

Biocoenoses were stored in ethanol, taphocoenoses were dried at room temperature and stored in micro cells. Ostracods (carapaces, valves, and `living´) were sorted by juveniles and adults. Different juvenile stages were not distinguished.

Species identification was based in most cases on valve morphology according to Meisch (2000), Fuhrmann (2012), and Wennrich (2005). Soft part analysis was performed in cases were species could not be identified from valves only (e.g., *F. fabaeformis, F. holzkampfi, H. incongruens* and *I. gibba*). All ostracod valves were counted (carapace = two valves) and relative abundances (percentage of the sum of valves in each sample) were calculated. Counted ostracods from the two fractions (500 µm and 250 µm) were added together.

Data analyses

Spearman`s rank correlation test was applied to identify relation among relative abundances of living assemblages and physico-chemical parameters.

Canonical correspondence analysis (CCA) was used to investigate the relationships between the distribution of living ostracod assemblages and physical and chemical environmental parameters. Relative abundances of species and four environmental variables including water temperature, electrical conductivity, oxygen content and pH, were used for the CCA.

To calculate Fisher´s α diversity and richness of the ostracod species in the different water bodies, the absolute numbers of taphocoenoses of all three months were summed for each

187 species. Additionally, to identify specific ostracod assemblages and determine habitat similarities
188 a cluster analysis was carried out.
189 Cluster analyses were performed based on relative abundances of the species, separately for
190 biocoenoses and taphocoenoses and for water bodies and species. As clustering algorithm,
191 Ward´s method to a Euclidian distance matrix was used. In all analyses, samples (water bodies)
192 containing less than 100 individuals were excluded. Furthermore, all species with overall
193 abundances ≤5% and occurring only in one site were also excluded from the analyses.
194 All statistical analyses were conducted using PAST version 3.25 (2019) (Hammer et al., 2001).
195
196
197 **3. Results**
198 ***Physico-chemical variables and habitat characteristics***
199
200 Water temperature (ranging from 8.6°C to 26.5°C) shows the strongest seasonal fluctuations
201 (highest values in June, lowest in April) (Fig 2 A). The lowest temperatures are provided by the
202 spring (QW). Salinity values (ranging from 0.7 to 20.75) of the former lake `Salziger See´ (KS,
203 BS, TE, TE2 and QW) provide generally higher values than localities outside this area (highest
204 values in September, lowest in April) (Fig 2 B). The other localities display constant values
205 during the sampling period.

206 Dissolved oxygen (DO) concentrations (ranging from 2.77 mg/l (OT2) to 19.4 mg/l (BS) are in
207 April in most localities higher than in the following months (Fig 2 C).

208 In all sites, pH values were ≥ 7 at each sampling site and reach a maximum of 8.9 in BS (Fig 2
209 D). The lowest value 7 was measured in the spring QW in September.

Substrate texture is dominated by sandy (e.g., BS and KS) and muddy substrate (e.g., TE, TA). Some localities are characterised by algae (SS), detritus (e.g., BS) or aquatic macrophytes (OT). Detailed information is summarised in Table 1.

Ostracod communities

General observations

Ostracods were found in all localities (and all samples). Living ostracods were found in eight out of ten water bodies in April, ten out of eleven in June, and nine out of ten in September. The relative abundance of bio- and taphocoenoses vary between the localities, and between the months. Compared to the previous months, number of valves and living ostracods were significantly lower in September. An extreme case was documented in a small pond (WS) where number of living ostracods decreased from several hundred (April 794, June 989) to only one specimen in September (Fig 3). Other localities provide a lower variation in living ostracod numbers (e.g., KS).

Species list

In total, 27 podocopid ostracod species were identified, twenty of them were also found living.

The following ostracod species were found (based on Meisch 2000):

Superfamily: Darwinuloidea Brady & Norman, 1889
Family: Darwinulidae Brady & Norman, 1889
Genus: *Darwinula* Brady & Robertson,1885
Darwinula stevensoni (Brady & Robertson, 1870)

Superfamily: Cypridoidea Baird, 1845
Family: Candonidae Kaufmann, 1900
Subfamily: Candoninae Kaufmann, 1900
Genus: *Candona* Baird, 1845
Candona candida (O.F. Müller, 1776)

240 *Candona neglecta* Sars, 1887
241 Genus: *Fabaeformiscandona* Krstić, 1972
242 *Fabaeformiscandona fabaeformis* (Fischer, 1851)
243 *Fabaeformiscandona holzkampfi* (Hartwig, 1900)
244 Genus: *Pseudocandona* Kaufmann, 1900
245 *Pseudocandona compressa* (Koch, 1838)
246 *Pseudocandona marchica* (Hartwig, 1899
247 Genus: *Candonopsis* Vavra, 1891
248 *Candonopsis kingsleii* (Brady & Robertson, 1870)
249 Subfamily: Cyclocypridinae Kaufmann, 1900
250 Genus: *Physocypria* Vavra, 1897
251 *Physocypria kraepelini* G.W. Müller, 1903
252 Family: Ilyocyprididae Kaufmann, 1900
253 Subfamily: Ilyocypridinae Kaufmann, 1900
254 Genus: *Ilyocypris* Brady & Norman, 1889
255 *Ilyocypris bradyi* Sars, 1890
256 *Ilyocypris gibba* (Ramdohr, 1808)
257 *Ilyocypris monstrifica* (Norman, 1862)
258 Family: Notodromadidae Kaufmann, 1900
259 Subfamily: Notodromadinae Kaufmann, 1900
260 Genus: *Notodromas* Lilljeborg, 1853
261 *Notodromas monacha* (O.F. Müller, 1776)
262 Family: Cyprididae Baird, 1845
263 Subfamily: Eucypridinae Bronstein, 1947
264 Genus: *Eucypris* Vavra, 1891
265 *Eucypris virens* (Jurine, 1820)
266 *Eucypris* sp?
267 Genus: *Prionocypris* Brady & Norman, 1896
268 *Prionocypris zenkeri* (Chyzer & Toth, 1858)
269 Subfamily: Herpetocypridinae Kaufmann, 1900
270 Genus: *Herpetocypris* Brady & Norman, 1889
271 *Herpetocypris chevreuxi* (Sars, 1896)
272 Subfamily: Cyprinotinae Bronstein, 1947
273 Genus: *Heterocypris* Claus, 1892
274 *Heterocypris incongruens* (Ramdohr, 1808)
275 *Heterocypris salina* (Brady, 1868)
276 Subfamily: Cypridopsinae Kaufmann, 1900
277 Genus: *Cypridopsis* Brady, 1867
278 *Cypridopsis vidua* (O.F. Müller, 1776)
279 Genus: *Plesiocypridopsis* Rome, 1965
280 *Plesiocypridopsis newtoni* (Brady & Robertson, 1870)
281 Genus: *Sarscypridopsis* McKenzie, 1977
282 *Sarscypridopsis aculeata* (Costa, 1847)

283 Genus: *Potamocypris* Brady, 1870
284 *Potamocypris arcuata* (Sars, 1903)
285 *Potamocypris smaragdina* (Vavra, 1891)

286 Superfamily: Cytheroidea Baird, 1850
287 Family: Limnocytheridae Klie, 1938
288 Subfamily: Limnocytherinae Klie, 1938
289 Genus: *Limnocythere* Brady, 1867
290 *Limnocythere inopinata* (Baird, 1843)

291 Family: Cytherididae Sars, 1925
292 Genus: *Cyprideis* Jones, 1857
293 *Cyprideis torosa* (Jones, 1850)

294 Family: Loxoconchidae Sars, 1925
295 Genus: *Cytheromorpha* Hirschmann, 1909
296 *Cytheromorpha fuscata* (Brady, 1869)
297
298
299
300
301 ***Spatial and seasonal distribution***

302 *General remarks*

303 Spatial and seasonal distribution of the ostracod species of the Mansfeld lake area is displayed at
304 Fig 3. The species list is sorted by maximum salinity tolerance values according to Frenzel et al.
305 (2010). This results in five groups, each for the salinity ranges of ≤5, ≤10, ≤15, ≤20, and ≤25,
306 whereby group I refers to the lowest salinity values and group V to the highest. Within a group,
307 species are also sorted by increasing salinity tolerance. Water bodies were also classified in
308 ascending order according to salinity values. Category a includes water bodies outside the former
309 `Salziger See´ area. These water bodies have lower salinity values (0.7 to 4) and are
310 comparatively small. Category b consist of the water bodies within the former `Salziger See´
311 with higher salinity values (4.4 to 20.7), and are larger than the water bodies in category a
312 (except QW). Category c comprises SS, the largest lake in the study area, and MG, a section of a
313 ditch that encircles the former `Salziger See´. Both water bodies have low salinity values (0.9 to
314 1.3). All of the species are freshwater species (except *C. torosa* and *C. fuscata*), most of them are

found in group I (lowest salinity tolerance) and just a few species are in groups with higher salinity tolerances (group IV and V).

The water bodies display significant differences in terms of their species composition in bio- and taphocoenoses between the sampling months. The term abundances always refer to relative abundances.

April

Even if species richness is highest in group I, in April almost all species of this group occur only very sporadically and in very low abundances (mostly ≤5%). This is particularly clear in biocoenoses and slightly less pronounced in taphocoenoses (Fig 3).

In group II there is an increase in species richness and abundances in bio- and taphocoenoses. Especially in II a, two species occur in higher abundances (*C. vidua, L. inopinata*). In II b, species richness also increases, but abundances are still rather low (mostly ≤5%), especially in taphocoenoses, and also, but much less pronounced, in biocoenoses, due to higher appearances of *H. salina*.

Although group III includes only half as many species as group II, species are equally common and abundant in bio- and taphocoenoses. Here, as well, abundances in bio- and taphocoenoses are significantly higher in III a than in III b, where abundances especially in taphocoenoses are rather low (≤5%). In biocoenoses, the abundances of the species (*C. neglecta, D. stevensoni, P. kraepelini*) are slightly higher than in II b.

Higher abundances in II a and III a are mainly explained by three species (*C. vidua, L. inopinata* and *P. kraepelini*), which often and plentifully occur in both, bio- and taphocoenoses. Species belonging to group IV were not found living in April, although *S. aculeata* is the most abundant species in TE and TE2 in taphocoenoses (≤70%).

In V a, occurrences and abundances are very low (≤5% in taphocoenoses and ≤4% in bicoenoses), but approximately highest in bio- and taphocoenoeses of V b, which is caused by *C. torosa*.

In general, in category a the most common and abundant species in taphocoenoses are the same as in biocoenoses. For instance, *C. vidua* and*, P. kraepelini* are common and abundant, *L. inopinata* occurs locally but with high abundances, and *C. candida* is common but with low abundances and never found alive. In category b, *C. torosa* is the only common and abundant species in bio- and taphocoenoses. Generally, most of the common species are not very abundant (e.g., *C. candida, L. inopinata, H. salina*). Abundant species in taphocoenoses are not abundant in biocoenoses (*H. salina*, *I. gibba, S. aculeata*) and common and abundant species in biocoenoses are not in taphocoenoses (e.g., *H. salina, C. neglecta, D. stevensoni*).

June

In June the distribution of the species is much more inconsistent compared to April. In Group I (i.e., low salinity tolerant-species) comparatively few species (e.g., in comparison to group II) can be found again. Nevertheless, there are significantly more species in bio- and taphocoenoses than in April. Species with lowest salinity tolerances (uppermost species of group I) are particularly widespread. This applies to all three categories (a, b and c). Overall, in this group species are not only more common, there is also an increase in abundances, both in bio- and taphocoenoses. In group II, in all water bodies species are more common, and abundance of some species increases significantly (e.g., *L. inopinata, H. salina)*.

In II a, the species distribution mainly relies on the species with comparatively low salinity tolerances (*C. candida, N. monacha, C. vidua*) and the water bodies are nearly similar in their species composition in taphocoenoses. In biocoenoses species richness increase but abundances

361 are rather low (e.g., ≤4% for most species). In II b, on the other hand, the differences between the
362 water bodies are larger. Almost all species occur in KS and BS in taphocoenoses and in a lesser
363 degree in biocoenoses, while species are basically not apparent in the other water bodies. An
364 exception represents *H. salina*, which is common and abundant in all water bodies of II b, in bio-
365 and taphocoenoses. Abundances and richness in II c is similar to KS and BS, but a comparison is
366 difficult as this category only includes one water body and was not sampled in April.
367 In III a are only two of the four species of category a (*D. stevensoni* and *P. kraepelini*). But these
368 are very common and abundant in bio- and taphocoenoses. In III b the occurrence is more
369 dispersed and species in bio- and taphocoenoses are not very abundant. In IV a, species richness
370 decrease significantly (*S. aculeata* with ≤4%). In IV b two species (*H. incongruence* and *S.*
371 *aculeata*) occur with low abundances in bio- and taphocoenoses. In IV c no species was found.
372 Group V is dominated by *C. torosa*, in category a in very low numbers, but in category b and c it
373 is the most common and abundant species in bio- and taphocoenoses.
374 In general, in all of the three categories abundant species in biocoenoses are also abundant in
375 taphocoenoses (with few exceptions e.g., *C. vidua* in ST and *H. salina* in TE2).
376 *September*
377 In September, species in group I were found sporadically in the water bodies and only in very
378 low abundances. Except *P. marchica*, which occurs in category a alive and is also very abundant
379 in taphocoenoses.
380 In I b and c species are slightly more common and more often alive. Also in II a, the species
381 occur only very sporadically, but the abundances in biocoenoses increase slightly (due to *C.*
382 *vidua*). In taphocoenoses the abundance also increases due to the mass occurrence of *C. vidua*
383 and *L. inopinata*. In II b, species are more common in both bio- and taphocoenoses with a slight

increase in abundances in taphocoenoses, even if most of the species (e.g., *C. candida, L. inopinata, P. compressa*) occur in low abundances (≤5%). In particular, living species (e.g., *C. candida, C. vidua, L. inopinata*) are common but occur with low abundances (≤4%) in this group and category. In III c, just a few species (*C. candida, L. inopinata, H. salina*) occur and with low abundances, except of *C. vidua* which is the most common and abundant species in bio- and taphocoenoses. In III a are the highest abundances for these water bodies, although absolute numbers of specimens are generally very low. Taphocoenoses are characterized by *P. kraepelini*, which is very common and abundant. In taphocoenoses of III b, all species occur in KS but are nearly absent in the other water bodies and abundances are very low (all ≤5%). In biocoenoses the abundances increase (*C. neglecta* and *D. stevensoni* between 40-70%). In bio- and taphocoenoses of III c abundances are low (≤4 in biocoenoses and ≤5% in taphocoenoses) and species are not very common. In IV a and V a, just two species (*S. aculeata*, adults ≤40% and *C. torosa* with ≤5%) occur in one water body (OT2). In category IV b and c and V b and c, the same two species occur in bio- and taphocoenoses. *C. torosa* is the most abundant species in bio- and taphocoenoses and was found in all water bodies nearly.

Samples from September are characterized by lowest number of species, as *P. zenkeri*, *C. kingsleii*, *E. virens*, *F. fabaeformis*, *H. incongruens* and *P. newtoni* did not occur.

It should also be noted, that in September a relatively large number of species (in comparison to the previous month), not occurring in taphocoenoses are found in biocoenoses (e.g., *C. vidua, D. stevensoni, C. neglecta*). However, occurrences in the water bodies are similar to previous samplings.

In general, in all waterbodies most of the species that are abundant in taphocoenoses are also abundant in biocoenoses. But there are more exceptions in September than in the previous

months. In category a *C. vidua* for example is abundant species in OT2 in biocoenoses, but is not present in taphocoenoses, *L. inopinata* is the most abundant species in taphocoenoses in WL, but living specimens did not occur, instead *D. stevensoni* is dominant (but just with one living specimen) in biocoenoses, but is not present in taphocoenoses.

In category b most of the species that are abundant in biocoenoses are less abundant in taphocoenoses (≤4%), except *C. torosa* which is abundant in both.

In category c abundances of bio- and taphocoenoses correspond most closely.

In summary

Comparing the ostracod species of categories a and b (i.e., low vs. higher salinities), two patterns emerge. First, two species (*P. marchica* and *N. monacha*) occur exclusively in bio- and taphocoenoses of category a (low salinity), and two species (*P. compressa, I. gibba*) appear only in bio- and taphocoenoses of category b (higher salinity). All of these four species are recorded with low specimen numbers only. Another point relates to the abundances of species. Some species occur in both water body categories, but are common and abundant in one category only, while they occur sporadically and with low abundances (and mostly only in taphocoenoses) in the other category. Although there are fluctuations in the abundances of the water bodies between the months (especially in the absolute values), it is noticeable that two species of the biocoenoses (*C. vidua* and *P. kraepelini*) are common and mostly dominant in the water bodies with lower salinities (category a) in all months. The same applies for the water bodies with higher salinity (category b), the species here are *H. salina* and *C. torosa*. The same pattern can be observed in taphocoenoses.

Despite the lower salinity values, the ostracod assemblages of category c differ from category a. Peculiarly, the ostracod assemblages of category c represent a combination of category a and b, due to the occurrence of the most abundant species *C. vidua* and *C. torosa*.

There is another aspect, differentiating the water bodies from each other. There is a lower species richness in smaller water bodies, dominated by one species while other species provide only low abundances (e.g., in OT2, *P. kraepelini* exaggerates with 85% the other two species *F. holzkampfi*; 9% and *C. vidua*; 6% by far). This becomes particularly obvious in biocoenoses and is very stable during all months.

Contrary, in larger water bodies, species richness is significantly higher, while no species is clearly dominant and varies during the months. The ambiguous distribution of species can also be seen in the cluster analyses of water bodies and species (Fig 4). The cluster analysis of the biocoenoses reveals that the similarity of the water bodies depends on the seasonal distribution of the species. Each sampling (i.e., month) provides slightly different species composition contributing to distinct species assemblages. Thus, taken all together there are neither distinct types of water bodies (and related environmental conditions) nor specific living ostracod species assemblages (Fig 4 C, D).

The picture is somewhat clearer in taphocoenoses of the seven water body groups (Fig 4 A). More or less the three samplings of a water body form a group, mostly together with spatially close (or connected) water bodies (e.g., KS, BS, MG, SS are one group). Only WL and TA form separate groups, but are also more spatially distant from the other water bodies, and thus are more isolated. Cluster analysis of the species revealed only two groups that maybe can be associated with an environmental parameter (Fig 4 B). These are *P. kraepelini* and *C. vidua* occurring in lower saline water bodies as well as *I. gibba* and *H. salina* occurring in water bodies

with higher salinities. However, again, most species (nine) are in one group showing no species-specific preferences and four species (*L. inopinata, P. marchica, S. aculeata* and *C. torosa*) are separate.

Seasonal population structure

For the seasonal population structure combined data from all species (adult: juvenile of living: dead ratios of assemblages) collected at each sampling site are considered (Fig 5). There is no generalized pattern in distribution of adults and juveniles in taphocoenoses and biocoenoses in the water bodies. Ratios of relative abundances for living:dead and adult:juveiles were different for the water bodies and between the sampling months. Some localities show relatively constant ratios through the sampling period (e.g., KS, TE, SS), while others vary greatly (e.g., BS, TE2). In most water bodies the number of valves exceeds the number of living ostracods found (KS, TE, OT). But also significantly more living than valves were found in some waterbodies (and months) (BS in September, OT2 in April and September, MG). In taphocoenoses, some water bodies provided significantly more adults than juveniles (e.g., KS, WL) while juveniles exaggerate adults in other water bodies (e.g., QW, TA). In SS approx. equal numbers of living and valves were found. MG is the only water body, in which significantly more juveniles than adults were found.

Species Diversity

For diversity and richness data, taphocoenoses for all three months were considered together. Species diversity (i.e., Fisher´s α diversity) and richness show the same trend (Fig 6), whereby the richness shows partially lower values. Richness and Fisher´s α diversity also do not show a clear trend or pattern in relation to salinity. Up to 4, species richness and diversity decrease with

477 increasing salinity, following the pattern from Frenzel (2009). From 4, however, richness
478 increase, and has its maximum at 6. Diversity of species decreases again at values higher than 6.
479
480 ***Inferences on species life cycle***
481 Although only three samplings were made, covering only half a year, living ostracods show clear
482 differences in their abundance patterns (Fig 7). The time at which maximum and minimum
483 abundance of the species is attained, differs for most species and for the water bodies. For
484 instance, *C. torosa* shows a peak in April (KS, TE) and September (BS), minimum abundance is
485 in June in two water bodies (KS, BS) while the abundance is nearly invariable low in June and
486 September in another site (TE). While few juveniles were generally found in KS, they have
487 maximum abundance in April (TE) and September (BS). An extreme case is displayed by *L.*
488 *inopinata*, which is highly abundant in WL (>90% of the entire species assemblage) in April and
489 June, but disappear completely in September. In BS *L. inopinata* did not occur in April, but was
490 very abundant in June (>80%) and occur in lower abundances in September (10-20%). While *C.*
491 *vidua* show the same abundance pattern in OT and OT2 (peak in September, minimum in June),
492 relative abundances of these two water bodies vary extremely (OT 35-100%, OT2 4-25%).
493 *Physiocypris kraepelini* has a peak in April (OT) and June (KS, OT2) and a minimum in
494 September in all three water bodies (in OT no individuals were found). For the species *H. salina*,
495 generally few adult individuals were found (15%), both in BS, and in TE. Peaks are in April (BS)
496 and June (TE). *Darwinula stevensoni* shows a significant minimum in June (in KS), otherwise
497 the abundances of this species are high. Peaks are in September (KS and TA), but for TA due to
498 the high numbers of juveniles. The maximum of adults for TA is in June. *Heterocypris salina*
499 (TE) and *D. stevensoni* (September in TA) are the only species of which more juveniles than

adults were found. Each species displays a different abundance distribution over the months in the water bodies. To obtain a general trend, the total species abundances of all waters were considered together (Supplementary Figure S1). For example, the total abundances show, that three species (*D. stevensoni, H. salina, L. inopinata*) are most abundant in June, while three (*C. torosa, C. vidua, P. kraepelini*) species have their minimum in June. Moreover, conclusions about the preservation potential of the valves of these species are possible by additional examination of the taphocoenoses of each species. In *C. torosa*, for example, the number of valves exaggerate living ones, which is also displayed by *H. salina, C. vidua*, and to a lesser degree in *P. kraepelini*. In *L. inopinata* and *D. stevensoni*, on the other hand, more living specimens than valves were found.

Species distribution and environmental conditions

Living ostracods occur in the Mansfeld lakes at salinity range between 0.7 and 11.5 (Fig 8). Most species are associated with values between 1 to 6. Only three species (*H. incongruens, H. salina* and *I. gibba*) occur at values up to 11.5. *H. salina* shows the highest tolerance to salinity (1.4-11.5).

Living ostracods were found in a temperature range between 9.4 up to 26.5°C. On average, most species were found between temperatures from 10 to 24 °C. Five species (*C. candida, F. fabaeformis, I. monstrifica, L. inopinata, N. monacha* and *S. aculeata*) occur in warmer water bodies (>18°C). The dissolved oxygen values, at which living ostracods were found, range between 4.3 mg/l and 19.4 mg/l. Majority of species occur between 5 and 16 mg/l. Although the range of most species is high, there are more species associated with lower dissolved oxygen

values. Only three species (*C. neglecta, C. torosa* and *H. salina*) were found living at values over 19 mg/l.

The pH range under which living ostracods were found is between 7.2 and 8.9. Most species are present between 7.5 and 8.6. Three species (*C. neglecta, C. torosa* and *H. salina*) occur in the entire pH range.

The canonical correspondence analysis plot (Fig 9) displays the relationships between physico-chemical parameters, ostracod species and localities. The first axis explains with 60% most of the variation and can be correlated with the parameters pH, temperature and dissolved oxygen. The second axis explains 22.5% of the variation and can be correlated with conductivity. However, only a few species show a significant correlation with the measured parameters (Supplementary Table S2).

D. stevensoni correlates with pH (r=0.56, p=0.02) and dissolved oxygen (r=0.57, p=0.02)*, L. inopinata* with temperature (r=0.53, p=0.03) and *P. marchica* (r=0.54, p=0.02) with dissolved oxygen. Two species correlate with salinity, *H. salina* (r=0.51, p=0.03) and *S. aculeata* (r=0.57, p=0.02). Nevertheless, no (habitat specific) groups can be distinguished in the CCA.

4. Discussion

General aspects on ostracod species distribution

All ostracod species found are reported as cosmopolitan, euryoecious freshwater species, and are typical for central Europe (Fuhrmann, 2012; Meisch, 2000), and in particular for the region Mansfeld (Pint et al., 2015; Wennrich, 2005). Due to the natural salinity of the lakes, the occurrence of the two brackish water species *C. fuscata* (only valves) and *C. torosa* are not uncommon and already previously documented (Pint et al., 2012; Wennrich, 2005). So far, no

548 living *C. torosa* from (saline) inland occurrences in Germany are known, although valves of *C.*
549 *torosa* have been found in higher saline water bodies in central Germany (Pint et al., 2012;
550 Scharf et al., 2017). The disappearance of *C. torosa* in Mansfeld area was explained by the
551 draining of the `Salziger See´ in 1892 (Fuhrmann, 2012; Scharf et al., 2017) and also Pint et al.
552 (2012; 2015) were not able to find living *C. torosa* in the region. Therefore, the high numbers of
553 living individuals of *C. torosa* found, especially in lower saline water bodies, are remarkable.
554 With 27 species found in the Mansfeld area, with a maximum of 17 species in one site (and
555 maximum of nine living), the number of species is relatively high with regard to the size of the
556 study area and the small size of the water bodies. Size of the region (and number of water
557 bodies) is decisive for the number of species found (Altınsaçlı, 2001; Külköylüoğlu et al., 2012;
558 Rossetti et al., 2004). Species richness and diversity of a water body f depends, on size of the
559 water body (Marchegiano et al., 2017; Rossetti et al., 2006; Valls et al., 2016), connectivity of
560 water bodies, type of habitat and related environmental conditions (Altınsaçlı, 2001;
561 Külköylüoglu et al., 2018; Külköylüoğlu and Vinyard, 2000)
562 and an interplay of different factors, such as substrate type, vegetation, food availability, season
563 and water depth (Smith and Delorme, 2010). The more ecological niches a water body has, the
564 more species can be found (Iglikowska and Namiotko, 2012). A comparison with studies from
565 marginal marine area also demonstrates that diversity and richness are dependent on the size of
566 the study area (Frenzel, 2009; Remane, 1934). The fluctuations between the water bodies of
567 diversity and richness are significantly lower, and the trend observed in the marginal marine area
568 of a decrease in richness with increasing salinity is not observed in the Mansfeld area. This
569 shows that the relationship between richness and salinity is scale-dependent. High species

richness usually indicates undisturbed habitats and stable environmental conditions (Carbonel et al., 1988; Valls et al., 2016).

For an evaluation, however, species composition must also be considered. As previously mentioned, most of the species occurring in the Mansfeld lake area are considered as widespread generalists with regard to their ecological preferences (in particular the common and abundant species). Actually, it is stated that cosmopolitan species often occur in disturbed habitats with low water conditions (Ghaouaci et al., 2017; Külköylüoğlu, 2013). Our data confirm this assumption, especially at the `Süßer See´, and at the residual lakes of the former `Salziger See´. Due to mining activities in the region during the last 800 years, soil and waters are exposed to high levels of pollutants from geological sources, but also anthropogenic pollutants from mine tailings and smelting products of copper shale mining (Becker et al., 2001; Frühauf, 1999). In particular, `Süßer See´ is considered as a sink for heavy metals (Becker et al., 2001). In addition, there are also considerable nitrogen and phosphate inputs from intensively agricultural use of the region (Lewandowski et al., 2003; Schmidt et al., 2010).

Spatial distribution of ostracod species

Although the occurring ostracod species are reported to have wide and rather unspecific ecological preferences, each water body is characterised by specific ostracod species assemblages. Despite some water bodies are more similar (e.g., water bodies of former `Salziger See´) in their assemblages than others (e.g., water bodies without former `Salziger See´), each water body shows specific species composition (and species richness) and abundances during the sampling period. These differences can be explained by different biotic and abiotic conditions

(Smith and Delorme, 2010). Cluster analysis of the taphocoenoses revealed that similarities could originate from the hydrological connection of some water bodies (SS, KS, BS and MG). The differentiation between living ostracods and valves displayed that species relative abundance and richness is much higher in valves, which might related to the different temporal scales integrated by these two associations (Akita, 2016; Valls et al., 2016). Biocoenoses represent short-term population dynamics and associated environmental conditions at the time the sample was taken and are therefore strongly influenced by the seasonality or life-cycle, respectively, of the species (Winegardner et al., 2015). Taphocoenoses, on the other hand, integrate, through accumulation and time averaging, several generations over seasons and years and species which are rare or absent in biocoenoses (e.g., *P. zenkeri, E. virens*) and accumulate, thus, a species assemblages corresponding to a larger range of environmental fluctuations (Levi et al., 2014; Poquet et al., 2007). Taphocoenoses not only contain ostracods through time, but also intra- and inter-habitat migrations (by water fowls or wave motion) are captured (spatial factor) (Mezquita et al., 2005; Winegardner et al., 2015). The Mansfeld lake area is not only a bird sanctuary with numerous water fowl species, it is also a staging and wintering site, water fowls and bird's may influence the intra- and inter-habitat dispersal of the species (Al Hussein et al., 2000). Also an air-born colonization of species by migratory birds, as it is also assumed for the foraminifer genus *Ammonia* and the ostracod species *C. fuscata*, is possible (Dieffenbacher-Krall, 2013; Wennrich et al., 2007).

This can lead to a distortion of the results of species distribution and related environmental inferences (Dieffenbacher-Krall, 2013).

The strong differences of species abundances highlight that the location of sampling within a water body is crucial. Sampling positions only a few meters away from each other can provide

615 significantly different live and dead species assemblages which might be caused by differences
616 in microhabitat conditions (Decrouy, 2009) and/or very local transport mechanisms. This could
617 be a reason why no living *C. torosa* has been found in the past few decades. The occurrence of
618 single ostracod species or populations in a water body can be restricted to very local areas
619 (Marchegiano et al., 2017; Smith and Delorme, 2010) and is not mandatorily related to changes
620 in water chemistry (i.e., temperature or salinity) as it is often assumed as in the case of *C. torosa*
621 (Pint et al., 2012). In order to obtain a comprehensive picture of the ostracod fauna, multiple
622 sampling should therefore ideally be carried out. If only one sampling can take place at a site,
623 this site should be carefully selected in order to better classify the results.
624
625 ***Seasonal distribution of ostracod species***
626 The differences in abundances and occurrences of species in the samples show, that not only
627 sampling site but also the time (i.e., specific month) of sampling have an important influence on
628 the distribution and abundance of living species due to their specific life-cycles (Altınsaçlı et al.,
629 2015; Decrouy, 2009). Thereby, the species show an individual pattern of occurrence in each
630 water body. Heip's (1976) extensive investigations on the life cycle of *C. torosa* have shown that
631 this species produces one generation per year, with a minimum in April, followed by increase of
632 specimens, with a maximum peak between July and October. Even if in the Mansfeld area the
633 maximum in the water bodies varies (KS and TE in April, BS in September), all water bodies
634 show a minimum in June. Also, considering the summarized relative and absolute abundances
635 for all considered water bodies, a significant minimum is found in June (Supplementary Figure
636 S1). Although the peak in September corresponds with Heip´s observations, the population
637 should increase from April and not decrease progressively in June. Also the high adult

abundances in BS in September are remarkable, considering the low abundances of juveniles in June.

Cypridopsis vidua, D. stevensoni, H.salina as well as *L. inopinata* are reported to occur throughout the year, but are most abundant in the summer months (from May to October-November) (Meisch, 2000). In the Mansfeld area, all species can be found already in April, and partly in considerable numbers (especially *L. inopinata*). *L. inopinata* develops different abundances and overwintering strategies depending on whether they live in freshwater or saline water bodies and these populations never co-occur. Freshwater populations appear in April/May and disappear in October/November, while saline population overwinter (Geiger 1998). Variations in the temporal occurrence of *L. inopinata* in different water bodies (BS and WL) were also observed in the Mansfeld area. Whether these are caused by the different salinities (BS: 6.4, WL: 2.1) of the water bodies is uncertain, since no *L. inopinata* was found in BS in April, and also the disappearance of *L. inopinata* in WL in September cannot be explained. It should also be mentioned that in WL one male carapace was found, what probably indicates a rare male population (one male among about 1000 female) (Meisch, 2000).

The fact that *H. salina* produces two to three generations per year (over summer month) and has relatively short life cycles (about 45 days) could explain the high abundance of juveniles in all months (Meisch, 2000). Although *H. salina* has such short life cycles, comparatively few valves are found in the sediment (and predominantly juveniles). Taphocoenoses raw data show that *H. salina* was found relatively often as carapace in all water bodies in the area. For juveniles this suggests high mortality. Especially in TE the number of carapace is high, predominantly in June. This may be an indication of non-optimal conditions, and it suggests that valves and carapaces were less affected by transport in TE, compared to BS. The lifespan of *D. stevensoni* can range

from <1 to 4 years, depending on the temperature (Van Doninck et al., 2003). Studies in a water body in Belgium resulted in a life span of <1 year, with reproduction starting in April (completed in September), with a maximum in June/July and lower densities in winter (Van Doninck et al., 2003). The minimum in June of *D. stevensoni* in KS indicates a different population dynamic in this water body. In TA, the maximum in June fits the results from Belgium, but the high numbers of adults and especially juveniles in September are remarkable. Temperature of the water bodies (KS: 10-23°C, TA: 13-26°C, Belgium pond: March to August: 10-24°C) is nearly invariable, and therefore not sufficient to explain the heterogeneous population dynamics, in this case. Whether the life cycle of *D. stevensoni* is postponed, or lasts longer than that observed in Belgium, cannot be clarified using the data gathered.

Populations of *P. kraepelini* are reported to remain constant in size throughout the year (Meisch, 2000). In the Mansfeld area, however, there are fluctuations, with e.g. the drastic decrease of specimens in KS and OT, but also a general decrease of the population in June. The life cycle of some species could have been adapted to the climatic conditions (warm-toned mesoclimate) in the study area and, therefore, begins somewhat earlier or is postponed (*D. stevensoni*, *C. torosa*). In the case of *C. torosa* it could also be possible that there is more than one generation (possibly two) per year, as it is known from Mediterranean populations (Mezquita et al., 2000).

Although only three samplings were carried during the summer months at intervals of two to three months, some deviations in the life cycle of the species, with regard to the temporal occurrence of the species and their minimum and maximum abundance, are evident. However, conclusions on possible causes of these deviations, detailed studies covering a longer time period are required, which should be carried out at shorter intervals in order to record species life cycle with shorter life spans (e.g., *H. salina* 45 days, (Meisch, 2000)).

Inferences on taphonomical processes

Inferences can be drawn about the productivity and preservation potential of the particular sampling site considering the ratio of living to dead ostracods (Kidwell, 2013). Water bodies, valves outnumber livings provide higher productivity and preservation potential (e.g., KS, TE, OT). If the valves outnumber livings, or is nearly the same, this may have several causes. First, sampling time has an impact on species productivity (depending on the life-cycle) and hydrological conditions (e.g., extreme rainfall washes away valves) may also matter (Avnaim-Katav et al., 2021; Jorissen and Wittling, 1999). This is evident in the example of BS, where not only the number of livings (April: 1279 valves and 37 living; September: 102 valves and 731 living) increase extremely, but also the number of valves significantly decrease. Second, the habitat type, with regard to different water energy levels, is important (Frenzel and Boomer, 2005). While almost all the water bodies are lakes and ponds sampled in the shallow littoral, MG is a ditch sampled on its slope. Since here the living outnumbers the valves, it can be assumed that due to the slope and flow of the water most of the valves are removed from the sample site. Also, the substrate type and vegetation may also be important, as it also significantly affects the sample size (Danielopol et al., 2002). In most water bodies the substrate type is mud or sand. In SS, also sand was the substrate type, but the littoral bottom was covered with coarse gravel and large stones, which made sampling much more difficult. Thus, much smaller amounts of sediment were sampled, which probably influenced the ratio of living to valves in favour of the livings. In general, the sample composition was very different due to substrate type (mud, sand, gravel) and vegetation (reed- belt, die-back reed-belt and other plant remains). Additionally, the valves can have different preservation potential due to differences in hinge type, valve thickness and/or shape (Alin and Cohen, 2004; Avnaim-Katav et al., 2021). Some living species were not

found in the taphocoenoses of the respective water bodies (e.g., *C. vidua* and *D. stevensoni*). Especially valves of *D. stevensoni* are very thin and fragile and may have been relocated or destroyed (Meisch, 2000). *Cyprideis torosa* on the other hand, has relatively large, thick valves, which are therefore not transported so quickly and are easily preserved (De Deckker and Lord, 2017). Even if the number of living *C. torosa* is partly small in some water bodies, the valves can be found *en masse* in the sediment. Thus, the preservability of the valves also plays a role in which species (and in which abundances) are found.

But not only the ratio of valves to living revealed informations about the conditions, also the ratio of adults to juveniles of the taphocoenoses, can be used to conclude about taphonomic processes (Boomer et al., 2003). In most water bodies the adults are by a multiple higher than juveniles by (KS, BS, TE, OT, OT2, WL, ST, SS). Only two water bodies provided similar ratios (MG) or number of slightly higher juveniles than that of adults (TA). And only in two water bodies at one sampling time (TE in June and QW in June) juveniles outnumbers adults significantly. Again, the differences between the months of a water body probably have seasonal causes (e.g., lake level fluctuations, due to precipitation or evaporation). A higher number of adults in the taphocoenoses, and conversely a lower number of juveniles (especially the first instars), suggests post-mortem processes such as transport, relocation and destruction of the valves (Boomer et al., 2003). As the littoral of a waterbody is most affected by currents, wave motion, terrestrial run-off and seasonal water-level fluctuation (observed in WL and SS for example) (Gasith and Gafny, 1990; Peters and Lodge, 2009), taphocoenoses typically are composed mainly by adults and late juveniles, while early instars are resuspend to deeper waters (Zhai et al., 2015). Due to the location in the central German dry region, the water bodies are highly affected by long dry periods (with low water levels) and short extreme precipitation

events (and high run-offs with high nutrient inputs) (Schmidt et al., 2010). Assuming strong contrasts between dry periods and precipitation (events) which may associated with reworking of littoral sediments the high number of adults compared to juveniles is not exceptional. It would also explain why almost no valves were found in sieve residues <125 µm. Additionally, some species are represented by valves only in very low abundances and single locations (e.g., *P. zenkeri, E. virens*). These factors (e.g., only single valves from a species, higher adult: juvenile ratio) indicate, not only that the assemblages are strongly influenced by taphonomic processes, they also indicate a disturbed habitat and could be stressors for the species. (Padisák, 1993). Including the 125 µm fraction and differentiating juvenile stages could have been provide information, which components of each assemblage are most affected by transport and size sorting (Boomer et al., 2003).

Ecological inferences

According to Fuhrmann (2012) and Meisch (2000), most of the species found prefer warm stagnant or cool stagnant water bodies. However, this classification is not sufficient to explain the heterogeneous spatial distribution of the species in this study. The area is spatially very limited, deviations of abiotic parameters of the water bodies are relatively small and almost all species are assumed to have large tolerance ranges for (measurable) physico-chemical parameters. Thus, all species occurrences reflect the known range of physico-chemical parameters (Frenzel et al., 2010; Ruiz et al., 2013). Only *I. bradyi* was found living in higher saline waterbodies (up to 7.9) than the known range from literature (4.5). The higher range of *Potamocypris* is probably due to the mixing of two species resulting from the difficulty in distinguishing them from each other.

We need to inquire why not all species were found in all water bodies. This may have several reasons. Sampling of the water bodies may not cover the entire ostracod fauna of a water body (Poquet and Mesquita-Joanes, 2011), as probably indicated by higher numbers of species in the taphocoenoses and the deviations of species composition and abundances in bio- and taphocoenoses.

Water bodies could provide, e.g. due to different hydro(geo)logical condition, such as residence time, inflow and/or run off, different hydrochemical compositions, like major ion concentrations (Mezquita et al., 2001; Smith and Delorme, 2010) that could have a undetected control on the species distribution. Salinity only indicates the ion concentration, but not the ion composition, a closer determination of the major ions could help to clarify the distribution pattern (Smith and Horne, 2002). Ion composition is a well-established factor determining the species composition and affecting species distribution (Delorme, 2001; Mezquita et al., 2005; Pint et al., 2015).

Also, other not-measured (micro)habitat specific factors are possible, like substrate type, type and coverage of vegetation, food supply and flow energy (Kiss, 2007; Marchegiano et al., 2017; Mezquita et al., 2005).

However, not only habitat conditions, but also metacommunity dynamics (e.g., inter-/intraspecific competition source-sink dynamics, dispersal rates, mass and rescue effects) are important drivers in distribution, abundance and life-cycle of species and can contract the structuring role of environmental parameters, especially in cosmopolitan species (Guisan et al., 2010; Leibold et al., 2004). Species may migrate, for instance, to other microhabitats when the optimal niche is occupied, or competing species may develop contrary life-cycles to avoid competition (Carbonel et al., 1988).

This could imply that ostracod species considered within a small geographical scale are not predominantly controlled by the most commonly considered abiotic environmental parameters (i.e., salinity, pH, temperature) and that they are probably not as euryoecious or generalistic as assumed so far.

The two species found exclusively in low saline (*P. marchica* and *N. monacha*) and higher saline (*P. compressa* and *I. gibba*) water bodies are not (except for *P. marchica*) abundant (<4%) and their occurrence is not significant enough to distinguish water bodies with respect to salinity. *Pseudocandona marchica* is more abundant but shows no (negative) correlation with salinity in CCA. Two species, *C. vidua* and P. *kraepelini*, occur in higher abundances in lower salinity water bodies (category a) and also grouped together in the cluster analysis. However, they also show no correlation with salinity or other parameters in the CCA. In water bodies with higher salinities (category b), *H. salina* and *C. torosa* are particularly abundant, and the CCA also shows a correlation between *H. salina* and salinity. In the cluster analysis, *H. salina* grouped together with *I. gibba*. However, *H. salina* shows higher abundances only in one water body (TE), and *I. gibba* also generally occurs only in two water bodies (TE2 and QW). Moreover, *C. vidua*, *P. kraepelini*, and *H. salina* also occur in other water bodies and show only slight differences in abundance in some cases, especially in the taphocoenoses. This highlights the differences between bio- and taphocoenoses.

Considering correlations of the species with the measured parameters (Fig 9), together with the species abundances of the species, it emerges that only few species correlate with specific parameters (e.g., *L. inopinata* with temperature). However, the indifferent pattern of the species in the CCA indicates that species composition is water body-specific and not directly controlled by the measured parameters. Although the measured physico-chemical parameters salinity, pH,

797 temperature and oxygen content cannot explain the species distribution, the parameters probably
798 influence the population dynamics (e.g., lifespan, temporal occurrence).
799 In the Mansfeld area, not only the occurrence of *C. torosa* is surprising, but also its distribution.
800 *Cyprideis torosa* is biogeographically widespread, an ecologically opportunistic species and
801 occurs in salinity ranges from freshwater to hypersaline (De Deckker and Lord, 2017). Several
802 carapace characteristics (e.g., sieve-pore shape, size, noding, valve outline) and shell
803 geochemistry are linked to salinity (Boomer et al., 2016; Frenzel et al., 2017, 2012; Grossi et al.,
804 2017), therefor it has been utilized as index fossil to reconstruct palaeosalinity and -temperature
805 (e.g., Pint et al., 2012; Scharf et al., 2017). Nearly all studies of living *C. torosa* are from coastal
806 areas with brackish water conditions, e.g., Portugal (Cabral et al., 2017), Spain (Marco-Barba et
807 al., 2012; Mezquita et al., 2000), Belgium (Heip, 1976), and Germany (respectively North and
808 Baltic Sea) (Boomer et al., 2016; Frenzel et al., 2017; Keyser and Aladin, 2004; Scharf et al.,
809 2017) . This suggests that *C. torosa* occur in freshwater habitats and tolerate low salinity
810 conditions, but seems to prefer brackish waters.
811 In the Mansfeld area, *C. torosa* occurs only between 0.9 to 7.9, having the highest population
812 density at lowest saline water bodies (0.9 and 1.3). The position of *C. torosa* in the CCA near
813 coordinate origin indicates that it is not affected by measured physico-chemical parameters and
814 also in the cluster analyses *C. torosa* shows no similarities with other species. Further studies,
815 ideally covering marginal marine and inland lakes are therefore necessary to prove whether *C.*
816 *torosa* can be used as an indicator for salinity variability and -reconstructions since there could
817 be autecological differences between marginal-marine and (low saline) inland populations.
818 Wang *et al.* (2021) figure out that populations from different regions are adapted to local aquatic
819 environments and therefore develop specific preferences. Thus, the actual preference range of a

820 species may be locally very narrow. The above-mentioned examples show, this assumption is not
821 only restricted to a large spatial scale, but can also be valid on a local scale for spatially close
822 water bodies with different conditions, such as the Mansfeld area. So, each water body provides
823 a specific combination of biotic and abiotic conditions for ostracod species. As a result, species
824 seem to develop their specific population dynamics and/or different life-cycles, depending on the
825 conditions they encounter (Leibold et al., 2004). Thus, no habitat specific species assemblages
826 related to the documented physico-chemical parameters can be distinguished in this study.
827

828 **5. Conclusion**

829 This actualistic-autecological survey focuses on the spatial and temporal distribution of ostracod
830 assemblages in twelve saline inland water bodies with special emphasis to differences between
831 bio- and taphocoenoses.
832 The study area represents a set of several water bodies within a relatively small geographical
833 area. Affected by similar hydrological and climatological conditions, the investigated water
834 bodies provide a salinity range of 0.7 to 20.7. Accordingly, ostracod species distribution was
835 expected to predominantly reflect salinity gradients. But, analyses of species-environmental
836 relationships not only revealed that salinity is not a major control on the distribution of species
837 but also that there is no simple pattern in temporal-spatial ostracod species distribution. Thus,
838 although most of the occurring species are considered as ecological generalists, species are not
839 ubiquitous. Variations in physico-chemical parameters (temperature, conductivity, oxygen, and
840 pH) did not help to explain temporal-spatial distribution of the ostracod species. Inferences
841 regarding the species´ life-cycles are elusive, as there are (strong) differences between the water
842 bodies. Species may have developed water body specific life-cycles. Indices of postponed or

bivoltine life-cycles and occurrences in slightly saline inland waters of *C. torosa* differs from observations from marginal marine habitats. Detailed studies are required to improve the use/potential as (palaeo-) salinity proxy and to verify that it is the same species, since this is the first record of living *C. torosa* in German inland waters, so far.

Furthermore, the relationship between abundance and species composition of living ostracods and related taphocoenoses is not straightforward. Strong differences between biocoenoses and taphocoenoses occurred even within water bodies and on very short time scales. This indicated that taphonomic processes can be very local including transport and relocation (e.g., species loss, dispersal) and affect species assemblages even on short time scales (i.e., monthly). This must be taken into account when fossil material is interpreted terms of biodiversity, (palaeo-) limnological and (palaeo-) ecological conditions. Although the dataset is complex and provides many information, further studies are required (with e.g., shorter sampling interval, differentiation between juvenile stages) to capture all patterns lying below the species distribution. Our study provides insights about the complexity of ostracod species distribution in space and time. Therefore, in order to obtain reliable and conclusive data, ideally replicate sampling always should be carried out including a differentiation of living specimens and valves should be clearly indicated. This allows enhanced understanding of the spatial and temporal distribution ostracod species, and a clues of possible taphonomic processes. Future studies should include not only major ion composition of the ambient water but also factors that have received little attention in the past such as vegetation type, composition or texture of substrate, nutrient input, hydrologic conditions, and community dynamics. This will help to increase the understanding of species' autecology and finally improve the indicator potential of these generalists.

Acknowledgments

We thank Birgit Schneider and Sylvia Haeßner for her support at the laboratory. We are grateful to Renate Matzke-Karasz for her help identifying the species. Peter Frenzel is kindly acknowledged for his help with data analyses. David Horne, Peter Frenzel and one anonymous reviewer are thanked for their helpful remarks to improve the manuscript.

References

Akita L.G., Frenzel P., Wang J., Börner N. & Peng P. (2016). Spatial distribution and ecology of the Recent Ostracoda from Tangra Yumco and adjacent waters on the southern Tibetan Plateau: A key to palaeoenvironmental reconstruction. *Limnologica* **59**, 21–43. https://doi.org/10.1016/j.limno.2016.03.005

Al Hussein I.A., Dietze R., Hartenauer K., Huth J., Lübke-Al Hussein M., Meyer F., *et al.* (2000). Die Tierwelt im Gebiet des ehemaligen Salzigen Sees. *Naturschutz im Land Sachsen-Anhalt* **37**, 24–43.Alin, S.R., Cohen, A.S., 2004. The live, the dead, and the very dead: taphonomic calibration of the recent record of paleoecological change in Lake Tanganyika, East Africa. Paleobiology 30, 44–81. https://doi.org/10.1666/0094-8373(2004)030<0044:tltdat>2.0.co;2

Altınsaçlı S. (2001). The Ostracoda (Crustacea) fauna of lakes Erikli, Hamam, Mert, Pedina and Saka (Iğneada, Kirklareli, Turkey). *Turkish Journal of Zoology* **25**, 343–355.

Altınsaçlı S., Perçin-Paçal F. & Altınsaçlı S. (2015). Assessments on diversity, spatiotemporal distribution and ecology of the living ostracod species (Crustacea) in oligo-hypersaline coastal wetland of Bargilya (Milas, Muğla, Turkey). *International Journal of Fisheries and Aquatic Studie* **3**, 357–373.

Avnaim-Katav S., Almogi-Labin A., Herut B., Kanari M. & Guy-Haim T. (2021). Benthic foraminifera from the Southeastern Mediterranean shelf: Dead assemblages and living-dead comparisons recording consequences of Nile River damming. *Marine Micropaleontology* **164**. https://doi.org/10.1016/j.marmicro.2021.101977

Baillie J.E.M., Collen B., Amin R., Akcakaya H.R., Butchart S.H.M., Brummitt N., *et al.* (2008). Toward monitoring global biodiversity. *Conservation Letters* **1**, 18–26. https://doi.org/10.1111/j.1755-263x.2008.00009.x

Becker A., Klöck W., Friese K., Schreck P., Treutler H.-C., Spettel B., *et al.* (2001). Lake Süßer See as a natural sink for heavy metals from copper mining. *Journal of Geochemical Exploration* **74**, 205–217. https://doi.org/10.1016/S0375-6742(01)00185-6

Boomer I., Frenzel P. & Feike M. (2016). Salinity-driven size variability in Cyprideis torosa (Ostracoda, Crustacea). *Journal of Micropalaeontology* **36**, 63–69. https://doi.org/10.1144/jmpaleo2015-043

Boomer I.A.N., Horne D.J. & Slipper I.A.N.J. (2003). The use of ostracods in Palaeoenvironmental studies, or what can you do with an ostracod shell? *Paleontological Society Paper* **9**, 153–180.

Cabral M.C., Fatela F., Lopes V., Freitas M.C. & Andrade C. (2017). Cyprideis torosa (Jones, 1850) in mainland Portugal: what do we know? . *Journal of Micropalaeontology* **36**, 94–112. https://doi.org/10.1144/jmpaleo2015-031

Carbonel P., Colin J.P., Danielopol D.L., Löffler H. & Neustrueva I. (1988). Paleoecology of limnic ostracodes: A review of some major topics. *Palaeogeography, Palaeoclimatology, Palaeoecology* **62**, 413–461. https://doi.org/10.1016/0031-0182(88)90066-1

Cardoso P., Erwin T.L., Borges P.A.V. & New T.R. (2011). The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation* **144**, 2647–2655. https://doi.org/10.1016/j.biocon.2011.07.024

Danielopol D.L., Ito E., Wansard G., Kamiya T., Cronin T.M. & Baltanas A. (2002). Techniques for Collection and Study of Ostracoda. In: *The Ostracoda:Applications in Quaternary Research*. (Eds A.R. Chivas & J.A. Holmes), pp. 65–97.

De Deckker P. & Lord A. (2017). Cyprideis torosa : a model organism for the Ostracoda? . *Journal of Micropalaeontology* **36**, 3–6. https://doi.org/10.1144/jmpaleo2016-100

Decrouy L. (2009). Environmental and Biological Controls on the Geochemistry (δ 18 O, δ 13 C, Mg/Ca, and Sr/Ca) of Living Ostracods from Lake Geneva. PhD thesis, University of Lausanne.

Delorme L.D. (2001). Ostracoda. *Ecology and Classification of North American Freshwater Invertebrates* **2**, 811–848.

Dieffenbacher-Krall A.C. (2013). Plant macrofossil methods and studies. Surface Samples, Taphonomy, Representation. In: *Encyclopedia of Quaternary Science*, 2nd edn. pp. 684–689. Elsevier.

Frenzel P. (2009). Die Ostrakoden und Foraminiferen der Ostsee und ihre Nutzung in den Geowissenschaften. Habilitation thesis, University of Jena.

Frenzel P. & Boomer I. (2005). The use of ostracods from marginal marine, brackish waters as bioindicators of modern and Quaternary environmental change. *Palaeogeography, Palaeoclimatology, Palaeoecology* **225**, 68–92. https://doi.org/10.1016/j.palaeo.2004.02.051

Frenzel P., Ewald J. & Pint A. (2017). Salinity-dependent sieve pore variability in Cyprideis torosa : an experiment . *Journal of Micropalaeontology* **36**, 57–62. https://doi.org/10.1144/jmpaleo2016-009

Frenzel P., Keyser D. & Viehberg F.A. (2010). An illustrated key and (palaeo)ecological primer for Postglacial to Recent Ostracoda (Crustacea) of the Baltic Sea. *Boreas* **39**, 567–575. https://doi.org/10.1111/j.1502-3885.2009.00135.x

Frenzel P., Schulze I. & Pint A. (2012). Noding of Cyprideis torosa valves (Ostracoda) - a proxy for salinity? New data from field observations and a long-term microcosm experiment. *International Review of Hydrobiology* **97**, 314–329. https://doi.org/10.1002/iroh.201211494

Frühauf M. (1999). Das Mansfelder Land - Kontrastraum zwischen landschaftlichen " Highlights ", Umweltbelastung und sozialen sowie wirtschaftlichen Problemen. *Hercynia N.F.* **32**, 161–190.

Fuhrmann R. (2012). Atlas quartärer und rezenter Ostrakoden Mitteldeutschlands, Altenburger Naturwissenschaftliche Forschungen.

Gasith A. & Gafny S. (1990). Effects of Water Level Fluctuation on the Structure and Function of the Littoral Zone. pp. 156–171.

Ghaouaci S., Yavuzatmaca M., Külköylüoğlu O. & Amarouayache M. (2017). An annotated checklist of the non-marine ostracods (Crustacea) of Algeria with some ecological notes.

954 *Zootaxa* **4290**, 140–154. https://doi.org/10.11646/zootaxa.4290.1.8
955 Grossi F., Prato S. Da & Gliozzi E. (2017). Is the occurrence of a sigmoidal ventral border in
956 Cyprideis torosa (Jones) valves linked to salinity? A morphometrical analysis approach .
957 Journal of Micropalaeontology 36, 70–79. https://doi.org/10.1144/jmpaleo2016-018
958 Guisan A., Thuiller W. & Zimmermann N.E. (2010). What Drives Species Distributions? In:
959 *Habitat Suitability and Distribution Models*. pp. 21–40. Cambridge University Press,
960 Cambridge.
961 Hammer Ø., Harper D.A.T. & Ryan P.D. (2001). PAST : Paleontological Statistics Software
962 Package for Education and Data Analysis PAST : PALEONTOLOGICAL STATISTICS
963 SOFTWARE PACKAGE FOR EDUCATION AND DATA ANALYSIS. *Palaeontologia*
964 *Electronica* **4**, 1–9.
965 Heip C. (1976). The Life-Cycle of Cyprideis torsa (Crustacea, Ostracoda). *Oecologia* **24**, 229–
966 245.
967 Horne D.J., Cohen A. & Martens K. (2002). Taxonomy, morphology and biology of quaternary
968 and living ostracoda. *Geophysical Monograph Series* **131**, 5–36.
969 https://doi.org/10.1029/131GM02
970 Horne D.J., Meisch C. & Martens K. (2019). Arthropoda. In: *Thorp and Covich's Freshwater*
971 *Invertebrates*, Fourth Edi. pp. 725–760. Elsevier.
972 Iglikowska A. & Namiotko T. (2012). The impact of environmental factors on diversity of
973 Ostracoda in freshwater habitats of subarctic and temperate Europe. *Annales Zoologici*
974 *Fennici* **49**, 193–218. https://doi.org/10.5735/086.049.0401
975 John H., Meyer F., Rauchhaus U. & Weiß G. (2000). Historie, aktuelle Situation und
976 Entwicklungsperspektiven der Salzflora am ehemaligen Salzigen See (Mansfelder Land).
977 *Herzynia* **33**, 219–244.
978 Jorissen F.J. & Wittling I. (1999). Ecological evidence from live-dead comparisons of benthic
979 foraminiferal faunas off Cape Blanc (Northwest Africa). *Palaeogeography,*
980 *Palaeoclimatology, Palaeoecology* **149**, 151–170. https://doi.org/10.1016/S0031-
981 0182(98)00198-9
982 Keyser D. & Aladin N. (2004). Noding in Cyprideis torosa and its causes. *Studia Quaternaria*
983 **21**, 19–24
984 Kidwell S.M. (2013). Time-averaging and fidelity of modern death assemblages: Building a
985 taphonomic foundation for conservation palaeobiology. *Palaeontology* **56**, 487–522.
986 https://doi.org/10.1111/pala.12042
987 Kiss A. (2007). Factors affecting spatial and temporal distribution of Ostracoda assemblages in
988 different macrophyte habitats of a shallow lake (Lake Fehér, Hungary). *Hydrobiologia* **585**,
989 89–98. https://doi.org/10.1007/s10750-007-0631-8
990 Külköylüoğlu O. (2013). Diversity, distribution and ecology of nonmarine Ostracoda (Crustacea)
991 in Turkey: Application of pseudorichness and cosmoecious species concepts. *Transworld*
992 *Research Network India Recent Res. Devel. Ecol* **4**, 1–18.
993 Külköylüoğlu O., Sari N. & Akdemir D. (2012). Distribution and ecological requirements of
994 ostracods (Crustacea) at high altitudinal ranges in Northeastern Van (Turkey). *Annales de*
995 *Limnologie* **48**, 39–51. https://doi.org/10.1051/limn/2011060
996 Külköylüoğlu O. & Vinyard G.L. (2000). Distribution and ecology of freshwater Ostracoda (
997 Crustacea) collected from springs of Nevada, Idaho, and Oregon : a preliminary study.
998 *Western North American Naturalist* **60**, 291–303.
999 Külköylüoglu O., Yavuzatmaca M., Akdemir D., Çelen E. & Dalkiran N. (2018). Ecological

classification of the freshwater ostracoda (crustacea) based on physicochemical properties of waters and habitat preferences. *Annales de Limnologie* **54**, 1–11. https://doi.org/10.1051/limn/2018017

Külköylüoğlu O., Yılmaz S. & Yavuzatmaca M. (2017). Comparison of Ostracoda (Crustacea) species diversity, distribution and ecological characteristics among habitat types. *Fundamental and Applied Limnology* **190**, 63–86. https://doi.org/10.1127/fal/2017/0872

Leibold M.A., Holyoak M., Mouquet N., Amarasekare P., Chase J.M., Hoopes M.F., *et al.* (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters* **7**, 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Levi E.E., Çakiroğlu A.I., Bucak T., Odgaard B. V., Davidson T.A., Jeppesen E., *et al.* (2014). Similarity between contemporary vegetation and plant remains in the surface sediment in Mediterranean lakes. *Freshwater Biology* **59**, 724–736. https://doi.org/10.1111/fwb.12299

Lewandowski J., Schauser I. & Hupfer M. (2003). Long term effects of phosphorus precipitations with alum in hypereutrophic Lake Süsser See (Germany). *Water Research* **37**, 3194–3204. https://doi.org/10.1016/S0043-1354(03)00137-4

Marchegiano M., Gliozzi E., Ceschin S., Mazzini I., Adatte T., Mazza R., *et al.* (2017). Ecology and distribution of living ostracod assemblages in a shallow endorheic lake: The example of Lake Trasimeno (Umbria, central Italy). *Journal of Limnology* **76**, 469–487. https://doi.org/10.4081/jlimnol.2017.1478

Marco-Barba J., Ito E., Carbonell E. & Mesquita-Joanes F. (2012). Empirical calibration of shell chemistry of cyprideis torosa (Jones, 1850) (Crustacea: Ostracoda). *Geochimica et Cosmochimica Acta* **93**, 143–163. https://doi.org/10.1016/j.gca.2012.06.019

Martens K., Schön I., Meisch C. & Horne D.J. (2008). Global diversity of ostracods (Ostracoda, Crustacea) in freshwater. *Hydrobiologia* **595**, 185–193. https://doi.org/10.1007/s10750-007-9245-4

Meisch C. (2000). Freshwater Ostracoda of Western and Central Europe. In: *Süßwasserfauna von Mitteleuropa*, 8(3). (Eds J. Schwoerbel & P. Zwick), pp. 1–522. Spektrum Akademischer Verlag, Heidelberg.

Mezquita F., Griffiths H.I., Domínguez M.I. & Lozano-Quilis M.A. (2001). Ostracoda (Crustacea) as ecological indicators: A case study from Iberian Mediterranean brooks. *Archiv fur Hydrobiologie* **150**, 545–560. https://doi.org/10.1127/archiv-hydrobiol/150/2001/545

Mezquita F., Olmos V. & Oltra R. (2000). Population ecology of Cyprideis torosa (Jones, 1850) in a hypersaline environment of the Western Mediterranean (Santa Pola, Alacant) (Crustacea: Ostracoda). *Ophelia* **53**, 119–130. https://doi.org/10.1080/00785236.2000.10409442

Mezquita F., Roca J.R., Reed J.M. & Wansard G. (2005). Quantifying species-environment relationships in non-marine Ostracoda for ecological and palaeoecological studies: Examples using Iberian data. *Palaeogeography, Palaeoclimatology, Palaeoecology* **225**, 93–117. https://doi.org/10.1016/j.palaeo.2004.02.052

Outhwaite C.L., Gregory, R.D., Chandler, R.E., Collen, B., Isaac, N.J.B., (2020). Complex long-term biodiversity change among invertebrates, bryophytes and lichens. *Nature Ecology and Evolution* **4**, 384–392. https://doi.org/10.1038/s41559-020-1111-z

Padisák J. (1993). The influence of different disturbance frequencies on the species richness, diversity and equitability of phytoplankton in shallow lakes. *Hydrobiologia* **249**, 135–156. https://doi.org/10.1007/BF00008850

1046 Peters J.A. & Lodge D.M. (2009). Littoral zone. In: *Encyclopedia of Inlandwaters*, Vol. 3. (Ed.
1047 G. Likens), pp. 79–87. Elsevier, Oxford.
1048 Pint A., Frenzel P., Fuhrmann R., Scharf B. & Wennrich V. (2012). Distribution of Cyprideis
1049 torosa (Ostracoda) in Quaternary Athalassic Sediments in Germany and its Application for
1050 Palaeoecological Reconstructions. *International Review of Hydrobiology* **97**, 330–355.
1051 https://doi.org/10.1002/iroh.201111495
1052 Pint A., Frenzel P., Horne D.J., Franke J., Daniel T., Burghardt A., *et al.* (2015). Ostracoda from
1053 inland waterbodies with saline influence in central Germany: Implications for
1054 palaeoenvironmental reconstruction. *Palaeogeography, Palaeoclimatology, Palaeoecology*
1055 **419**, 37–46. https://doi.org/10.1016/j.palaeo.2014.07.042
1056 Pint A., Schneider H., Frenzel P., Horne D.J., Voigt M. & Viehberg F. (2017). Late Quaternary
1057 salinity variation in the Lake of Siebleben (Thuringia, Central Germany) – Methods of
1058 palaeoenvironmental analysis using Ostracoda and pollen. Holocene 27, 526–540.
1059 https://doi.org/10.1177/0959683616670216
1060 Poquet J.M. & Mesquita-Joanes F. (2011). Combined effects of local environment and
1061 continental biogeography on the distribution of Ostracoda. *Freshwater Biology* **56**, 448–
1062 469. https://doi.org/10.1111/j.1365-2427.2010.02511.x
1063 Poquet J.M., Mezquita F., Rueda J. & Miracle M.R. (2007). Loss of Ostracoda biodiversity in
1064 Western Mediterranean wetlands. *Aquatic Conservation: Marine and Freshwater*
1065 *Ecosystems* **656**, 636–656. https://doi.org/10.1002/aqc
1066 Rice, E.W., Baird, R.B., Eaton, A.D., 2017. Standard Methods for the Examination of Water and
1067 Wastewater, 23rd ed. American Public Health Association, American Water Works
1068 Association, Water Environment Federation. https://doi.org/10.5860/choice.37-2792
1069 Remane A. (1934). Die Brackwasserfauna (mit besonderer Berücksichtigung der Ostsee).
1070 *Verhandlungen der Deutschen Zoologischen Gesellschaft*, 34–74.
1071 Rossetti G., Bartoli M. & Martens K. (2004). Limnological characteristics and recent ostracods
1072 (Crustacea, Ostracoda) of freshwater wetlands in the Parco Oglio Sud (Northern Italy).
1073 *Annales de Limnologie* **40**, 329–341. https://doi.org/10.1051/limn/2004030
1074 Rossetti G., Martens K., Meisch C., Tavernelli S. & Pieri V. (2006). Small is beautiful: Diversity
1075 of freshwater ostracods (Crustacea, Ostracoda) in marginal habitats of the province of
1076 Parma (Northern Italy). *Journal of Limnology* **65**, 121–131.
1077 https://doi.org/10.4081/jlimnol.2006.121
1078 Ruiz F., Abad M., Bodergat A.M., Carbonel P., Rodríguez-Lázaro J., González-Regalado M.L.,
1079 *et al.* (2013). Freshwater ostracods as environmental tracers. *International Journal of*
1080 *Environmental Science and Technology* **10**, 1115–1128. https://doi.org/10.1007/s13762-
1081 013-0249-5
1082 Scharf B., Herzog M. & Pint A. (2017). New occurrences of Cyprideis torosa (Crustacea,
1083 Ostracoda) in Germany . *Journal of Micropalaeontology* **36**, 120–126.
1084 https://doi.org/10.1144/jmpaleo2015-022
1085 Schmidt G., Frühauf M. & Dammann S. (2010). Regional adaptation to climate change –
1086 supporting land management decisions in the Central German dry region by geoecological
1087 research. *The Problems of Landscape Ecology* **28**,111–122.
1088 Smith A.J. & Delorme L.D. (2010). Ostracoda. *Ecology and Classification of North American*
1089 *Freshwater Invertebrates*, 725–771. https://doi.org/10.1016/B978-0-12-374855-3.00019-4
1090 Smith A.J. & Horne D.J. (2002). Ecology of marine, marginal marine and nonmarine ostracodes.
1091 *Geophysical Monograph Series* **131**, 37–64. https://doi.org/10.1029/131GM03

Trost M. & Rauchhaus U. (2000). Die Lage und naturröumliche Einordnung des ehemaligen Salzigen Sees. In: LAU Sachsen-Anhalt (Hrsg.): *Der Salzige See, Naturschutz im Land Sachsen-Anhalt* **37**, 5–7.

Valls L., Zamora L., Rueda J. & Mesquita-Joanes F. (2016). Living and Dead Ostracod Assemblages in a Coastal Mediterranean Wetland. *Wetlands* **36**, 1–9. https://doi.org/10.1007/s13157-015-0709-4

Van Doninck K., Schön I., Martens K. & Goddeeris B. (2003). The life-cycle of the asexual ostracod Darwinula stevensoni (Brady & Robertson, 1870) (Crustacea, Ostracoda) in a temporate pond. *Hydrobiologia* **500**, 331–340. https://doi.org/10.1023/A:1024656920904

Viehberg F.A. (2005). Quantitative paleoenvironmental studies using freshwater ostracods in northeast Germany. PhD Thesis, University of Greifswald.

Wang C., Kuang X., Wang H., Guo G. & Song G. (2021). Ostracods as a proxy for paleoclimatic change: An essential role of bioculture experiment taking Limnocythere inopinata (Crustacea: Ostracoda) as an example. *Ecological Indicators* **121**, 107000. https://doi.org/10.1016/j.ecolind.2020.107000

Wennrich V. (2005). Die spätweichselglaziale und holozäne Klima- und Umweltgeschichte des Mansfelder Landes/ ehemaligen Salzigen Sees. PhD Thesis, University of Leipzig.

Wennrich V., Meng S. & Schmiedl G. (2007). Foraminifers from Holocene sediments of two inland brackish lakes in central Germany. *Der Salzige See: Naturschutz im Land Sachsen-Anhalt* **37**, 24–43. https://doi.org/10.2113/gsjfr.37.4.318

Wennrich V., Wagner B., Melles M. & Morgenstern P. (2005). Late Glacial and Holocene history of former Salziger See, Central Germany, and its climatic and environmental implications. *International Journal of Earth Sciences* **94**, 275–284. https://doi.org/10.1007/s00531-005-0468-1

Winegardner A.K., Beisner B.E., Legendre P. & Gregory-Eaves I. (2015). Are the landscape-level drivers of water column and surface sediment diatoms different? *Freshwater Biology* **60**, 267–281. https://doi.org/10.1111/fwb.12478

Zhai D., Xiao J., Fan J., Wen R. & Pang Q. (2015). Differential transport and preservation of the instars of Limnocythere inopinata (Crustacea, Ostracoda) in three large brackish lakes in northern China. *Hydrobiologia* **747**, 1–18. https://doi.org/10.1007/s10750-014-2118-8

Figure 1

Geographical location in Germany and sampling sites (red points) in the Mansfeld lake area. Outlines of the former Salziger See are taken from Trost & Rauchhaus 2000.

Abbreviations of the water bodies: KS=Kernersee, BS=Bindersee, TE=Teufe, TE2= Teufe2, QW=Quelle im Wald, OT=Ottilienteich, OT2= Ottilienteich2, WL=Wannsleben, TA=Tongrube Alte Schule, ST=Salzatal, SS=Süßer See, MG=Mittelgraben.

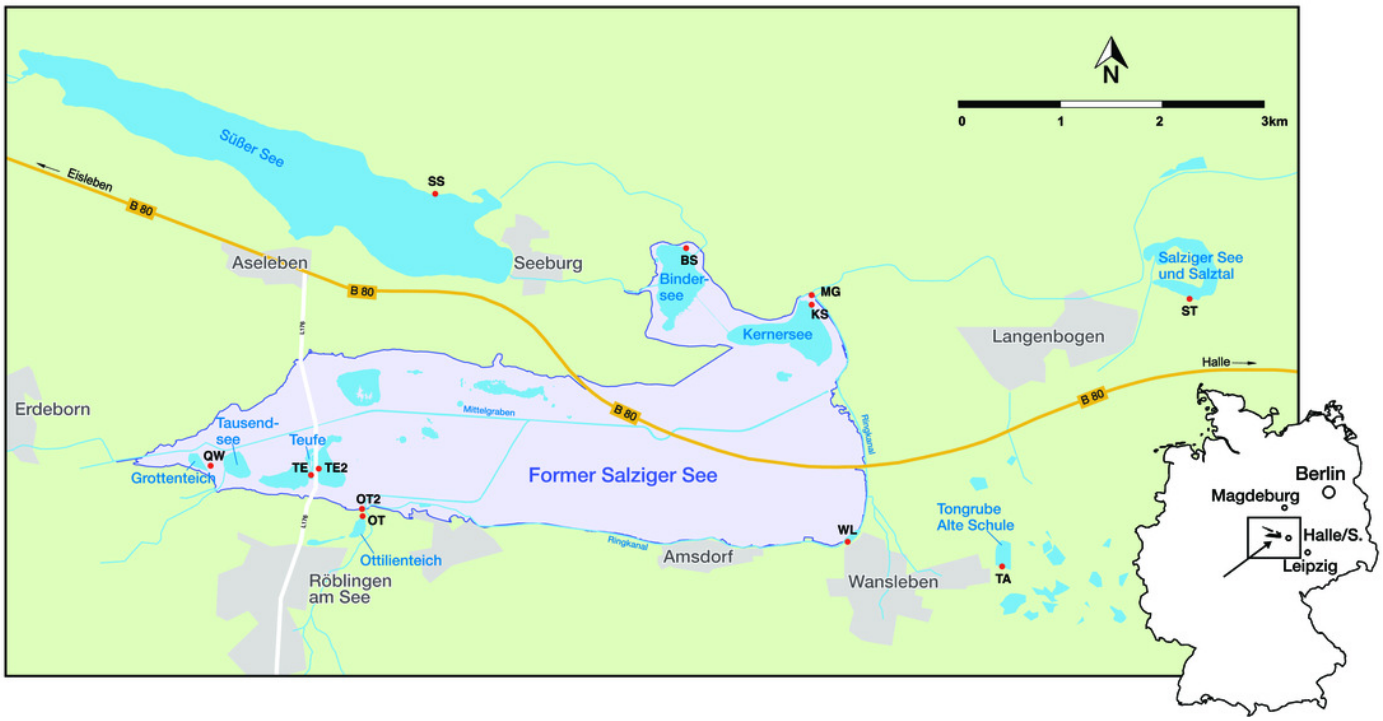

Figure 2

Physico-chemical parameters of the investigated water bodies in the Mansfeld lake area in terms of temperature, salinity, DO (dissolved oxygen) and pH.

Symbols represent: ♦=lake, += temporary source fed ditch section, ●=pond, ▲= ditch. Dashed lines separate waterbodies of the former `Salziger See´ (left) and water bodies outside (right). Abbreviations of the water bodies: KS=Kernersee, BS=Bindersee, TE=Teufe, TE2= Teufe2, QW=Quelle im Wald, OT=Ottilienteich, OT2= Ottilienteich2, WL=Wannsleben, TA=Tongrube Alte Schule, ST=Salzatal, SS=Süßer See, MG=Mittelgraben.

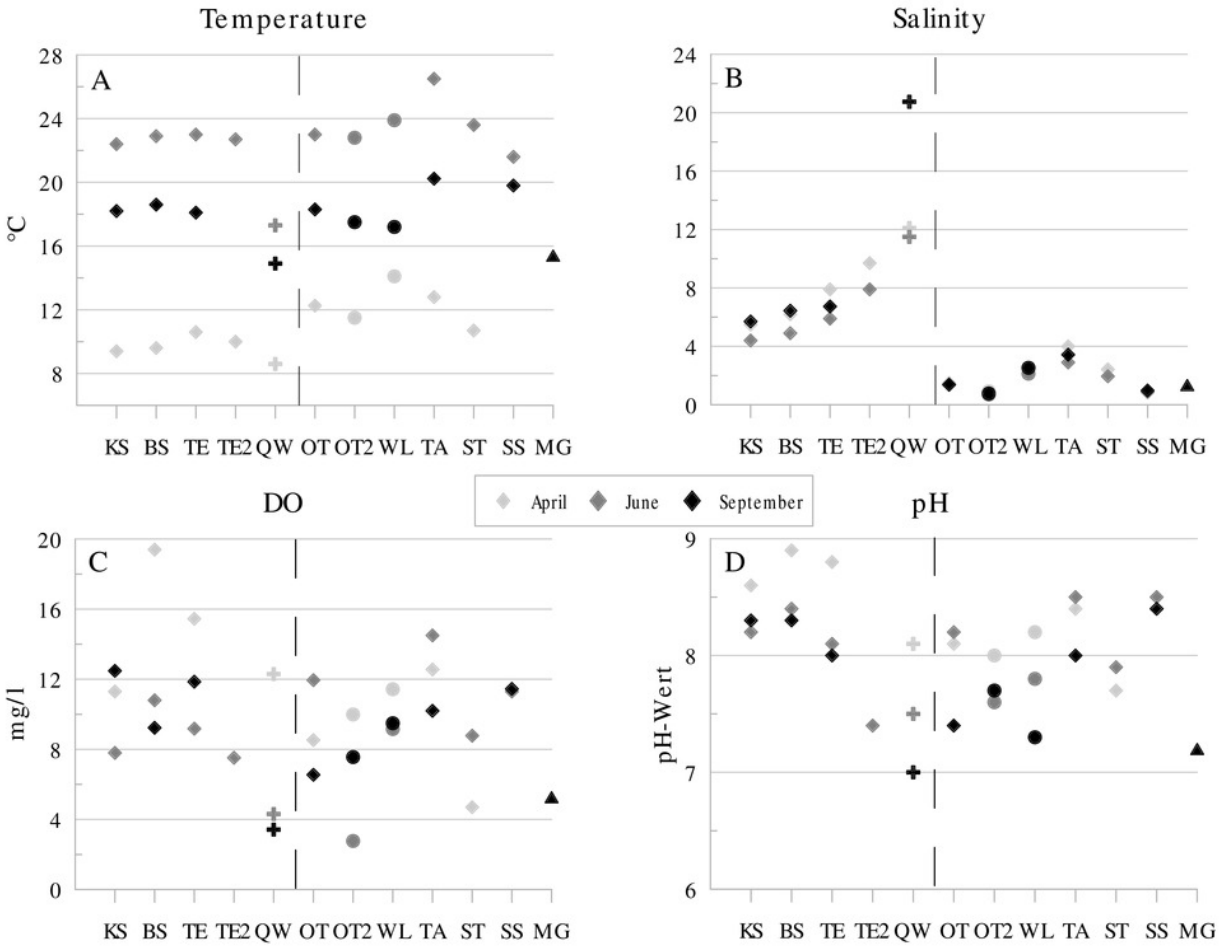

Figure 3

Relative abundances of taphocoenoses (circles) and biocoenoses (colours) of ostracod species, adult (a) and juveniles (j) in April, June, and September.

Abbreviations of the water bodies: KS=Kernersee, BS=Bindersee, TE=Teufe, TE2= Teufe2, QW=Quelle im Wald, OT=Ottilienteich, OT2= Ottilienteich2, WL=Wannsleben, TA=Tongrube Alte Schule, ST=Salzatal, SS=Süßer See, MG=Mittelgraben. Species code: Cc=*Candona candida*, Cn= *Candona neglecta*, Cf= *Cytheromorpha fuscata*. Ck= *Candonopsis kingsleii*, Ct=*Cyprideis torosa*, Cv= *Cypridopsis vidua*, Ds= *Darwinula stevensoni*, E sp?= *Eucypris* sp?, Ev= *Eucypris virens*, Ff= *Fabaeformiscandona fabaeformis*, Fh= *Fabaeformiscandonda holzkampfi*, Hc= *Herpetocypris chevreuxi*, Hi= *Heterocypris incongruens*, Hs= *Heterocypris salina*, Ib= *Ilyocypris bradyi*, Ig= *Ilyocypris gibba*, Im=*Ilyocypris monstrifica*, Li= *Limnocythere inopinata*, Nm= *Notodromas monacha*, Pk= *Physocypria kraepelini*, Pn= *Plesiocypridopsis newtoni*, Pa= *Potamocypris arcuata*, Ps= *Potamocypris smaragdina*, Pz= *Prionocypris zenkeri*, Psc= *Pseudocandona compressa*, Psm= *Pseudocandona marchica*, Sa= *Sarscypridopsis aculeata*.

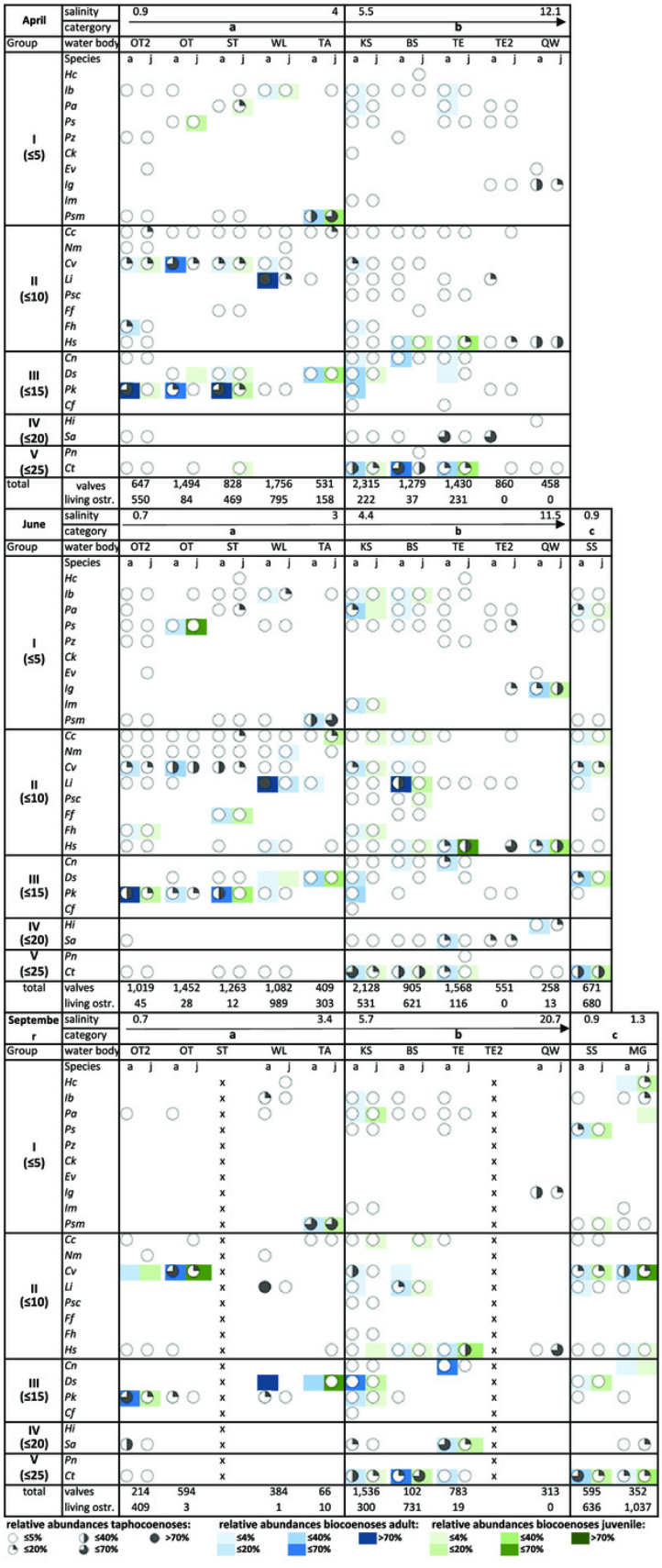
April
salinity 0.9 4 5.5 12.1
catergory a b
Group water body OT2 OT ST WL TA KS BS TE TE2 QW
Species a j a j a j a j a j a j a j a j a j a j
Hc Ib Pa Ps Pz Ck Ev Ig Im Psm
I (≤5)
Cc Nm Cv Li Psc Ff Fh Hs
II (≤10)
Cn Ds Pk Cf
III (≤15)
Hi Sa
IV (≤20)
Pn Ct
V (≤25)
total valves 647 1,494 828 1,756 531 2,315 1,279 1,430 860 458
living ostr. 550 84 469 795 158 222 37 231 0 0
June
salinity 0.7 3 4.4 11.5 0.9
category a b c
Group water body OT2 OT ST WL TA KS BS TE TE2 QW SS
Species a j a j a j a j a j a j a j a j a j a j a j
Hc Ib Pa Ps Pz Ck Ev Ig Im Psm
I (≤5)
Cc Nm Cv Li Psc Ff Fh Hs
II (≤10)
Cn Ds Pk Cf
III (≤15)
Hi Sa
IV (≤20)
Pn Ct
V (≤25)
total valves 1,019 1,452 1,263 1,082 409 2,128 905 1,568 551 258 671
living ostr. 45 28 12 989 303 531 621 116 0 13 680
September
salinity 0.7 3.4 5.7 20.7 0.9 1.3
category a b c
Group water body OT2 OT ST WL TA KS BS TE TE2 QW SS MG
Species a j a j a j a j a j a j a j a j a j a j a j a j
Hc Ib Pa Ps Pz Ck Ev Ig Im Psm
I (≤5)
Cc Nm Cv Li Psc Ff Fh Hs
II (≤10)
Cn Ds Pk Cf
III (≤15)
Hi Sa
IV (≤20)
Pn Ct
V (≤25)
total valves 214 594 384 66 1,536 102 783 313 595 352
living ostr. 409 3 1 10 300 731 19 0 636 1,037
relative abundances taphocoenoses: ≤5% ≤20% ≤40% ≤70% >70%
relative abundances biocoenoses adult: ≤4% ≤20% ≤40% ≤70% >70%
relative abundances biocoenoses juvenile: ≤4% ≤20% ≤40% ≤70% >70%

Figure 4

Cluster analyses of water bodies and species for taphocoenoses and biocoenoses.

A=taphocoenoses waterbodies, B=taphocoenoses specie, C=biocoenoses waterbodies, D=biocoenoses species. Abbreviations of the water bodies: KS=Kernersee, BS=Bindersee, TE=Teufe, TE2= Teufe2, QW=Quelle im Wald, OT=Ottilienteich, OT2= Ottilienteich2, WL=Wannsleben, TA=Tongrube Alte Schule, ST=Salzatal, SS=Süßer See, MG=Mittelgraben. Species code: Cc=*Candona candida*, Cn= *Candona neglecta*, Ct=*Cyprideis torosa*, Cv= *Cypridopsis vidua*, Ds= *Darwinula stevensoni*, Ff= *Fabaeformiscandona fabaeformis*, Hc= *Herpetocypris chevreuxi*, Hi= *Heterocypris incongruens*, Hs= *Heterocypris salina*, Ib= *Ilyocypris bradyi*, Ig= *Ilyocypris gibba*, Li= *Limnocythere inopinata*, Pk= *Physocypria kraepelini*, Pa= *Potamocypris arcuata*, Ps= *Potamocypris smaragdina*, Psm= *Pseudocandona marchica*, Sa= *Sarscypridopsis aculeata*. Roman numbers represent the different species- and water body groups.

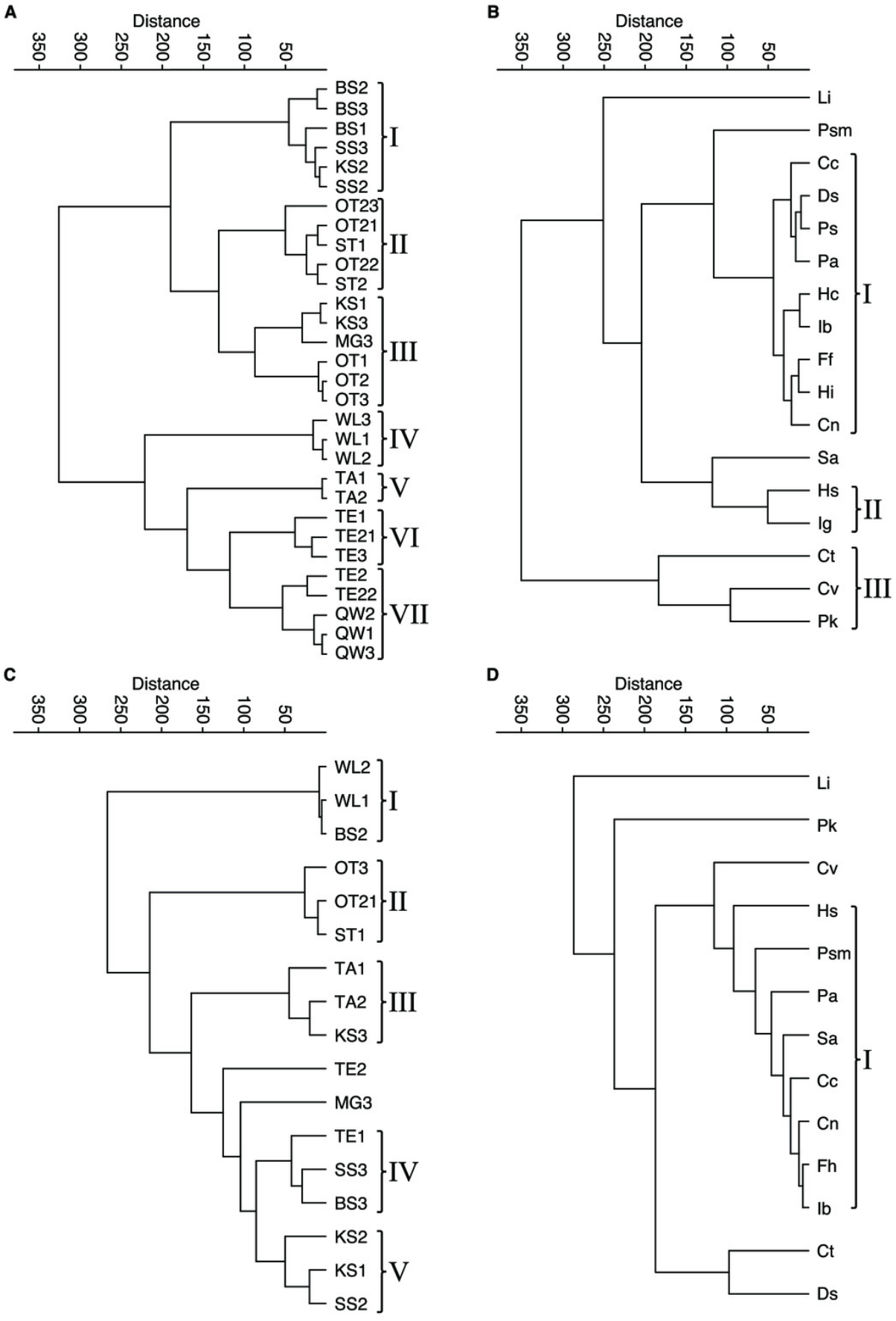
A
Distance
350
300
250
200
150
100
50
BS2
BS3
BS1
SS3
KS2
SS2
I
OT23
OT21
ST1
OT22
ST2
II
KS1
KS3
MG3
OT1
OT2
OT3
III
WL3
WL1
WL2
IV
TA1
TA2
V
TE1
TE21
TE3
VI
TE2
TE22
QW2
QW1
QW3
VII
B
Distance
350
300
250
200
150
100
50
Li
Psm
Cc
Ds
Ps
Pa
Hc
Ib
Ff
Hi
Cn
I
Sa
Hs
Ig
II
Ct
Cv
Pk
III
C
Distance
350
300
250
200
150
100
50
WL2
WL1
BS2
I
OT3
OT21
ST1
II
TA1
TA2
KS3
III
TE2
MG3
TE1
SS3
BS3
IV
KS2
KS1
SS2
V
D
Distance
350
300
250
200
150
100
50
Li
Pk
Cv
Hs
Psm
Pa
Sa
Cc
Cn
Fh
Ib
I
Ct
Ds

Figure 5

Ratios of adult and juvenile ostracod assemblages differentiated for bio-and taphocoenoses. Bars represent combined data from all species collected in each water bodies in April (A), June (J) and September (S).

Abbreviations of the water bodies: KS=Kernersee, BS=Bindersee, TE=Teufe, TE2= Teufe2, QW=Quelle im Wald, OT=Ottilienteich, OT2= Ottilienteich2, WL=Wannsleben, TA=Tongrube Alte Schule, ST=Salzatal, SS=Süßer See, MG=Mittelgraben.

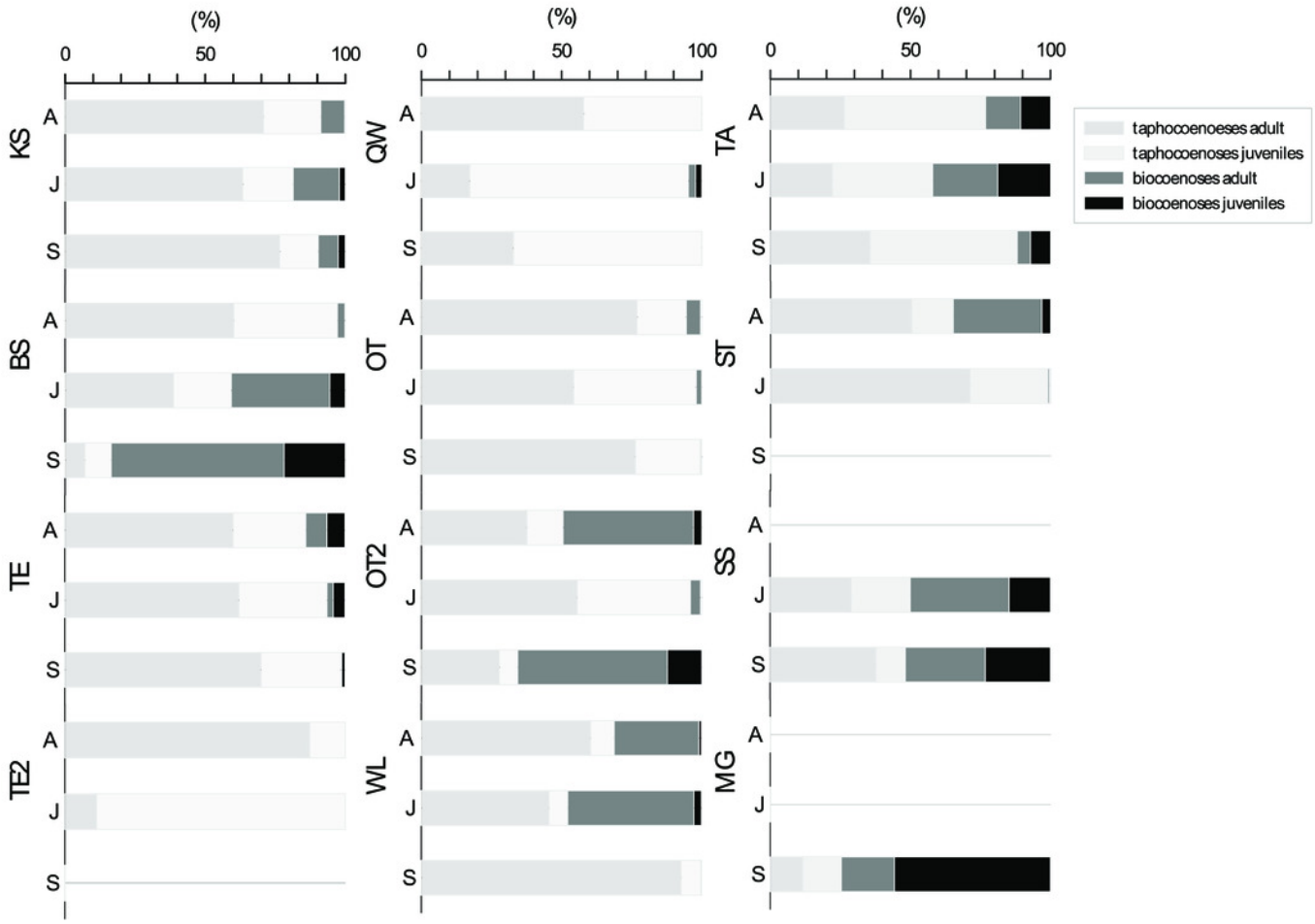

Figure 6

Fisher´s α diversity and richness of cumulated taphocoenoses of all sampled month of the water bodies at Mansfeld area in comparison with richness of freshwater species in waterbodies in the catchment of the Baltic Sea Frenzel (2009).

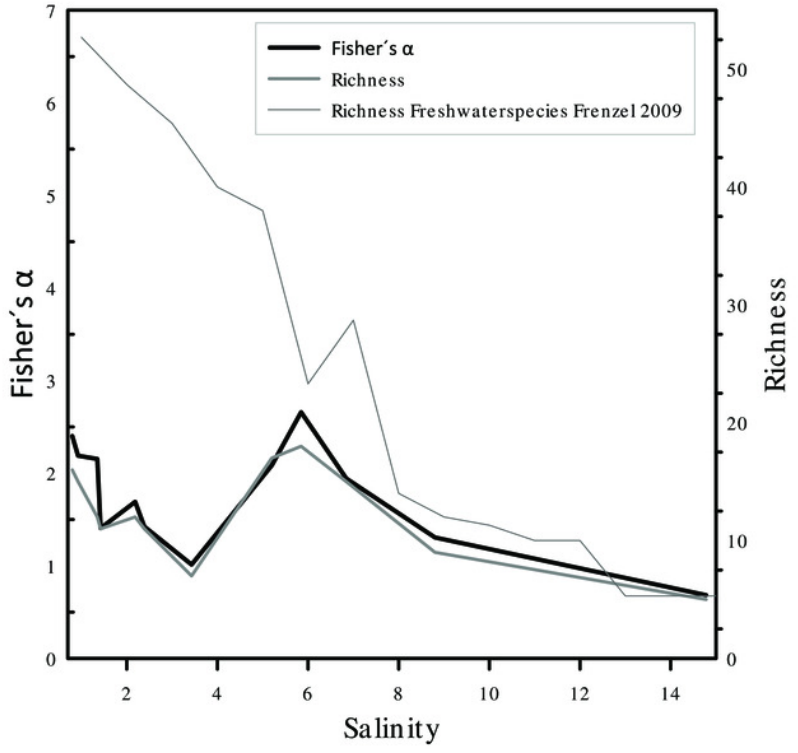

Figure 7

Seasonal distribution of selected most common and abundant living species in selected waterbodies differentiated for adult and juveniles in April (A), June (J) and September (S).

Abbreviations of the water bodies: KS=Kernersee, BS=Bindersee, TE=Teufe, TE2= Teufe2, QW=Quelle im Wald, OT=Ottilienteich, OT2= Ottilienteich2, WL=Wannsleben, TA=Tongrube Alte Schule, ST=Salzatal, SS=Süßer See, MG=Mittelgraben.

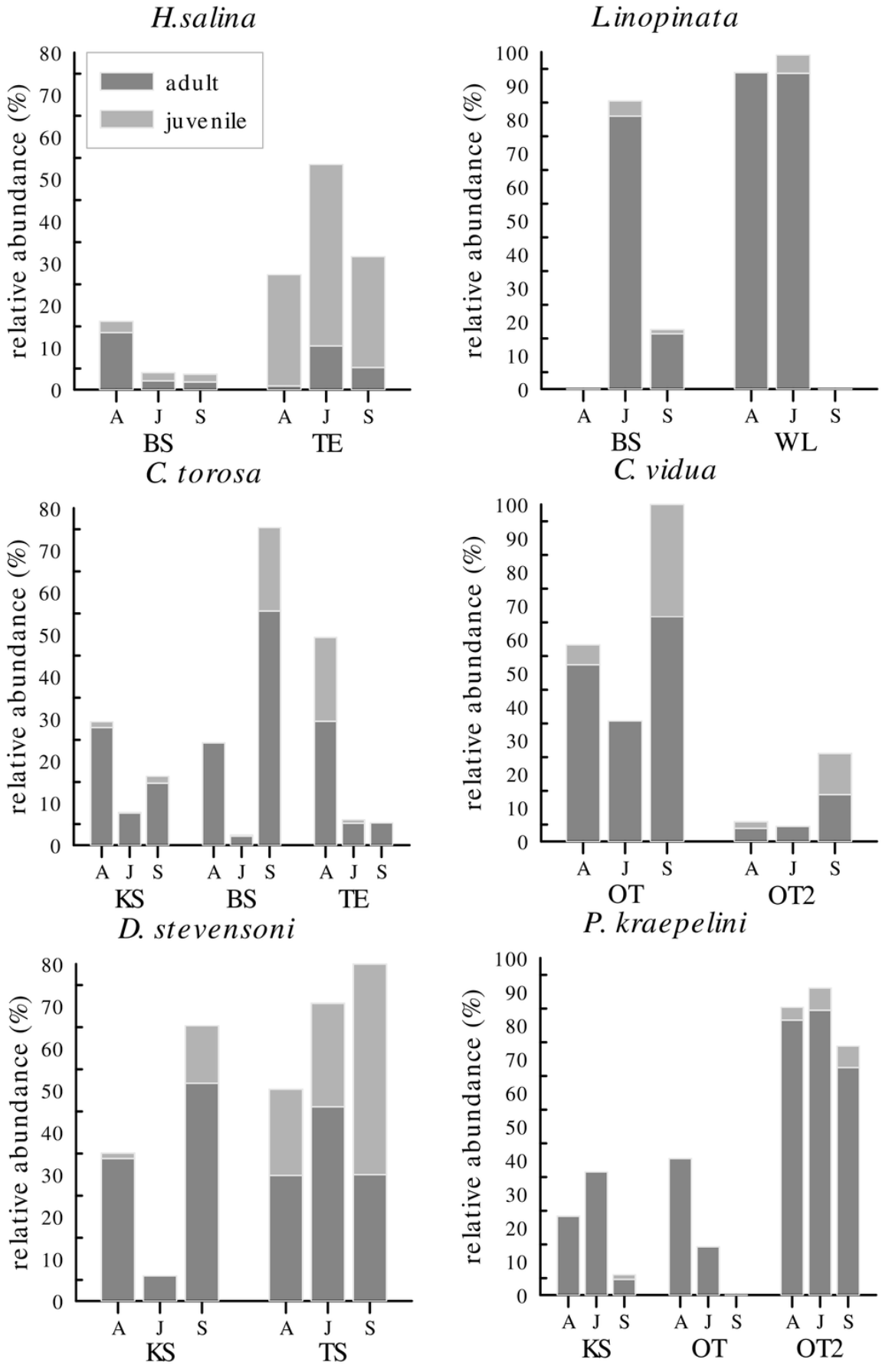
H.salina
adult
juvenile
relative abundance (%)
A J S A J S
BS TE
Linopinata
relative abundance (%)
A J S A J S
BS WL
C. torosa
relative abundance (%)
A J S A J S A J S
KS BS TE
C. vidua
relative abundance (%)
A J S A J S
OT OT2
D. stevensoni
relative abundance (%)
A J S A J S
KS TS
P. kraepelini
relative abundance (%)
A J S A J S A J S
KS OT OT2

Figure 8

Distribution of ostracod species in relation to variation ranges of salinity, temperature, dissolved oxygen, and pH inferred from all samplings and localities compared to the study of Frenzel et al 2010. Solid lines represent a known range, dashed lines r

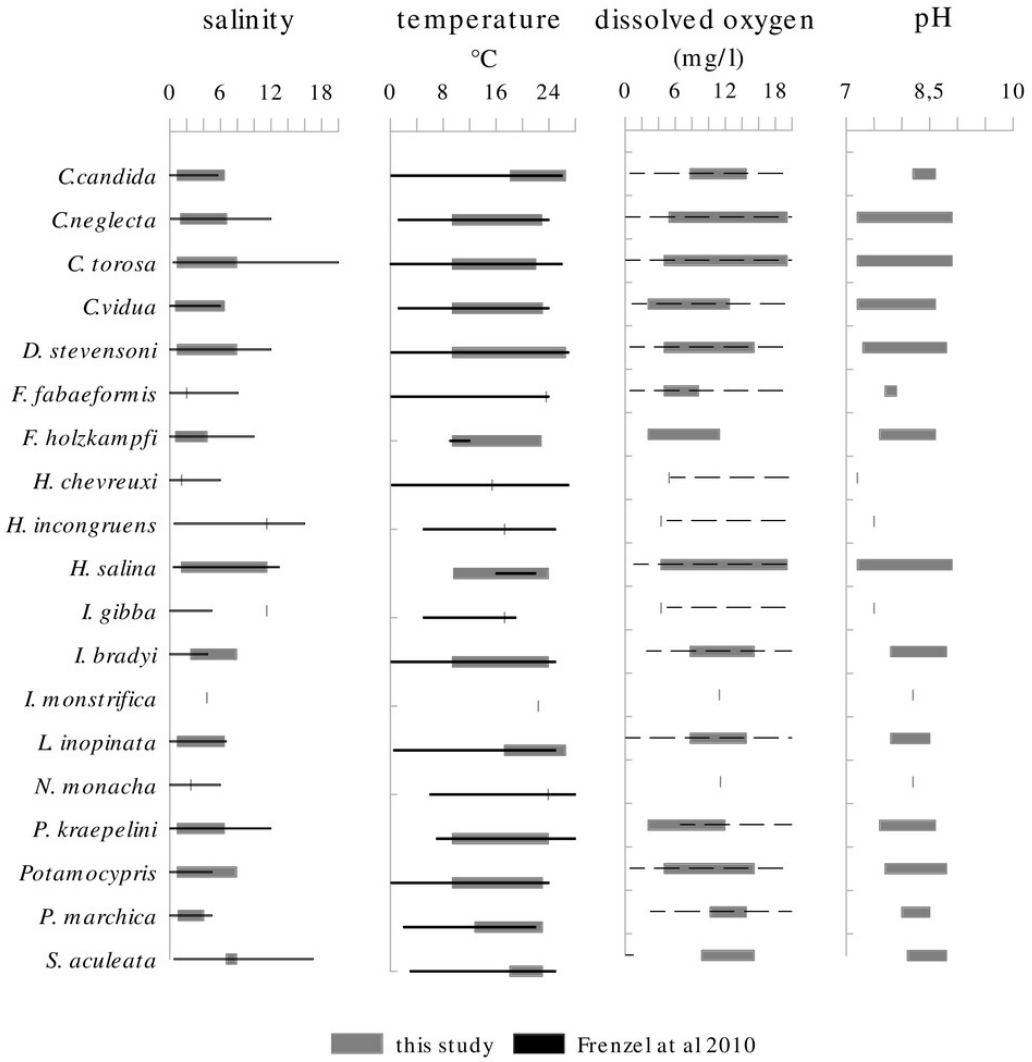
salinity
temperature
°C
dissolved oxygen
(mg/l)
pH
0 6 12 18
0 8 16 24
0 6 12 18
7 8,5 10
C.candida
C.neglecta
C. torosa
C.vidua
D. stevensoni
F. fabaeformis
F. holzkampfi
H. chevreuxi
H. incongruens
H. salina
I. gibba
I. bradyi
I. monstrifica
L. inopinata
N. monacha
P. kraepelini
Potamocypris
P. marchica
S. aculeata
this study
Frenzel at al 2010

Figure 9

First two axes of Canonical correspondence analysis (CCA) ordination plot of ostracods (▲), environmental variables (cond= conductivity, do=dissolved oxygen, temp= temperature and pH) and water bodies (●).

Abbreviations of the water bodies: KS=Kernersee, BS=Bindersee, TE=Teufe, TE2= Teufe2, QW=Quelle im Wald, OT=Ottilienteich, OT2= Ottilienteich2, WL=Wannsleben, TA=Tongrube Alte Schule, ST=Salzatal, SS=Süßer See, MG=Mittelgraben. Cc=*Candona candida*, Cn= *Candona neglecta*, Ct=*Cyprideis torosa*, Cv= *Cypridopsis vidua*, Ds= *Darwinula stevensoni*, Fh= *Fabaeformiscandonda holzkampfi*, Hs= *Heterocypris salina*, Ib= *Ilyocypris bradyi*, Li= *Limnocythere inopinata*, Pk= *Physocypria kraepelini*, Pa= *Potamocypris arcuata*, Psm= *Pseudocandona marchica*, Sa= *Sarscypridopsis*. Sample months are represented by numbers (1=April, 2=June and 3= September) following the water body abbreviation.

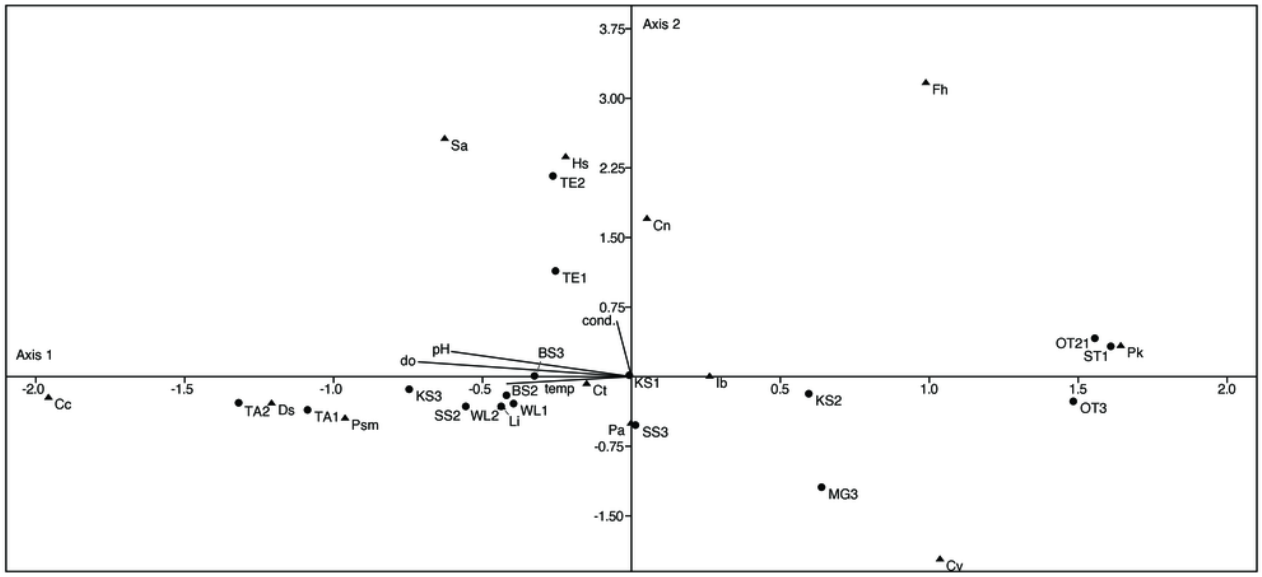

Table 1(on next page)

Overview of sampling sites in terms of name and water body abbreviations, coordinates, habitat type and sample month.

Sample month: A=April, J=June, S=September

Name	Abbreviation	Latitude (N)	Longitude (E)	habitat type	sample month
Kernersee	KS	51.485102	11.740385	open shoreline of a lake, sand	A/J/S
Bindersee	BS	51.489583	11.724183	reed-belt of the lake, sand with detritus	A/J/S
Teufe	TE	51.470694	11.675120	die-back reed-belt of the lake, muddy substrate (sludge)with other plant remains	A/J/S
Teufe 2	TE2	51.471072	11.676226	reed-belt of the lake, mud (sludge)	A/J
Quelle im Wald (spring in the woods)	QW	51.470166	11.668428	temporary source fed ditch section, mud with plant remains (rotten leaves)	A/J/S
Ottilienteich	OT	51.467471	11.682365	braced shoreline of the lake, dense growth of aqutic macrophytes, rarely sediment	A/J/S
Ottilienteich 2	OT2	51.468329	11.682151	open shoreline of the lake, sand	A/J/S
Wannsleben	WL	51.465623	11.744928	shallow shoreline of the pond, muddy substrate with gravel	A/J/S
Tongrube Alte Schule (Clay pit `old school´)	TA	51.463703	11.764960	open shoreline, muddy substrate with algea and macrophyts	A/J/S
Salzatal	ST	51.485483	11.790107	reed-belt of the lake, sand	A/J
Süßer See	SS	51.498387	11.676360	shallow shoreline, sand covered with coarse gravel, stones and algea	J/S
Mittelgraben	MG	51.485583	11.741115	ditch sampled on ist slope, muddy substrate with macrophytes	S

1