Primary Research Paper

Freshwater ostracod assemblages and their relationship to environmental variables in waters from northeast Germany

Finn A. Viehberg

Institut für Geographie und Geologie, Universität Greifswald, Friedrich-Ludwig-Jahn-Str. 17a, D-17487, Greifswald, Germany

Present Address: Laboratoire de paléolimnologie et de paléoécologie, Centre d'Études Nordiques, Pavilion Abitibi-Price, Université Laval, Sainte-Foy, Québec, G1K 7P4, Canada (*E-mail: finn.viehberg@cen.ulaval.ca*)

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Abstract

An ecological calibration dataset for freshwater ostracods from 33 localities throughout West-Pomerania (Mecklenburg-Vorpommern, Germany) was evaluated using multivariate statistical methods. A total of 47 freshwater ostracod species were identified. Nine species were rediscovered after 100 years since the last published record and Candonopsis scourfieldi and Pseudocandona sucki was recorded for the first time in the study area. Special emphasis is put on the phenology of each species to gain information on the water characteristics at the time of their last moult. Canonical correspondence analysis (CCA) revealed that the ecological variables such as water temperature, Ca, Mg, and lake area were statistically most significant (p < 0.005; n = 72) in explaining variation in the distribution of ostracod assemblages. In addition, a transfer function was developed for paleolimnological approaches, based on a weighted-averaging (WA) model to calculate water temperature from the relative abundances of 22 selected ostracod species. This model was successfully applied to infer lake water temperature from subfossil ostracod assemblages collected from lacustrine deposits in northeast Germany (Lake Krakower See).

Introduction

Research on freshwater ostracods started in Europe in the late 18th century (i.e., O.F. Müller, 1772). These small bivalved microcrustaceans were subject to numerous monographs of taxonomy and systematics, while initially only little attention was paid to ecological aspects. Redeke (1936) was one of the first who emphasized the ecology of single ostracod species. Recently, Meisch (2000) summarized new and already published ecological data of Western and Central-European species and it became apparent that the understanding of the fundamental or realized ecological niche for some ostracods still needs further investigation. This ecological knowledge is of great paleolimnological interest as preserved ostracod valves store valuable paleoenvironmental information for reconstruction purposes in Quaternary science. In this context, the use of ostracod analysis increased significantly over the past years and has been successfully applied to identifying changes in lake paleohydrology and reconstructing trophic status (e.g., Namiotko et al., 1993; Scharf, 1998), water level (e.g., Colman et al., 1994; Viehberg, 2004), water temperature (e.g., Colman et al., 1990; Forester, 1991), salinity (e.g., Gell et al., 1994; Boomer et al., 1996), and ion-composition (e.g., Forester, 1991; Smith et al., 1992).

Nevertheless, some authors regret that the use of ostracods as paleo-proxies remained more descriptive than precise over decades compared to other zoological indicators (e.g., Holmes, 2003). Due to this imprecision, subfossil ostracod valves are often used as a calcite source for analysis of stable isotopes (¹⁸O and ¹³C) or trace elements (Ca, Mg, Sr, and Mn) (e.g., Holmes & Chivas, 2002; Schwalb, 2003), rather than quantitative paleoindicators themselves.

Quantitative transfer functions need to be developed upon modern calibration datasets to fulfill the requirements of modern paleolimnological approaches. Some encouraging results have been published for North America (Alin & Cohen, 2003), South America (Mourguiart et al., 1998), and the Eastern Mediterranean (Külköylüoglu & Dügel, 2004), but an European equivalent is still missing. It is one task of this paper to initiate such an ecologically orientated database for northeast Germany and to present paleotemperature estimates inferred with the developed quantitative transfer function.

Materials and Methods

The study area is situated in West Pomerania and covers $8,633 \text{ km}^2$ in the northeast of Germany. A total of 33 lakes were sampled at 10-weeks intervals from 19.02.2002 to 24.08.2003 for living Ostracoda (Fig. 1; Table 1).



Figure 1. Study area (8,633 km²). Rural districts: DM = Demmin, NVP = North - Vorpommern, OVP = East - Vorpommern, $R\ddot{U}G = R\ddot{u}gen district$, UER = Uecker- Randow district; Cities: HGW = Greifswald, HST = Stralsund, NB = Neubrandenburg; Numbered squares = sampled lakes (1–33; coordinates, see Table 1); K3 = core KOS III (see text).

Table 1. Localities for calibration dataset. Listed from North to South with annotations to lake area and mean water depth

	max.	min.	mean	STDS
Area (10 ⁴ m ²)	3,255.8	6.2	234.9	662.6
Depth (m)	32.3	1.6	4.2	3.1
annual				
Water temperature (°C)	23.5	1.6	14.5	6.0
Ca (mg dm^{-3})	228.0	2.1	81.1	36.3
Mg (mg dm^{-3})	85.5	1.6	19.3	17.1
Winter (1.12. – 29.2.)				
Water temperature (°C)	5.9	1.6	3.5	1.69
Ca (mg dm^{-3})	106.1	62.7	83.5	18.5
Mg (mg dm^{-3})	33.4	12.8	20.2	8.1
Spring (1.3. – 31.5.)				
Water temperature (°C)	15.7	5.4	10.8	2.8
Ca (mg dm ⁻³)	228.0	2.1	80.4	44.0
Mg (mg dm^{-3})	83.7	1.6	19.8	19.3
Summer (1.6. – 31.8.)				
Water temperature (°C)	23.5	15.9	21.5	1.6
Ca (mg dm^{-3})	153.1	15.8	79.4	31.3
Mg (mg dm^{-3})	85.5	3.4	18.7	16.32
Autumn (1.9. – 30.11.)				
Water temperature (°C)	18.2	5.0	12.7	3.7
Ca (mg dm^{-3})	136.0	15.3	84.1	31.3
Mg (mg dm^{-3})	71.5	3.1	19.0	15.7

The lake basins of this study are situated north of the Pomeranian terminal moraine lobe (stage WII *sensu* Müller et al., 1995) in the till plains of the north eastern lowland. It is considered that most lakes were ice-free and recolonized by biota at the latest by 14,000 a BP when the buried dead ice finally melted (Kaiser, 2001).

Today, the landscape is mainly characterized by intensive agriculture, which is reflected by the generally increased nutrient load in surface water. Additionally, the carbonate concentration is high due to the soluble $CaCO_3$ content of the underlying moraines (Table 2). Most lakes are shallow (mean depth: 4.2 m; Table 1 + 2) and are not thermally stratified during the summer period (UM-MV, 1998).

In addition, water bodies close to the Baltic Sea shoreline revealed an increased conductivity (>1000 μ S cm⁻¹), caused either by brackish groundwater inflow or occasional water exchange.

The climate of the study area is influenced by both temperate North Atlantic as well as extreme continental elements. In addition, the Baltic Sea influences a 10–30 km wide strip along the coast (Duphorn et al., 1995). The annual mean daily temperature recorded at Stralsund and Neubrandenburg respectively is + 8.5 °C and + 7.9 °C, representing a transect through the study area. The mean annual precipitation for the area is 552 mm.

Sampling and laboratory techniques

The surface sediment was sampled randomly in the littoral zone of each lake with a simplified Kajakcorer (diameter 5.38 cm). The top 2 cm were placed into a white bowl with the overlying water. All ostracods were collected alive in the field with a water exhauster (Viehberg, 2002). Special care was taken to assure representative results. First, all swimming and fast moving species were collected to concentrate more easily on slow crawling species, which were also sucked by the exhauster. Finally, the bowl was tilted gently in all directions several times, so part of the sample was exposed to the air and submerged by the next counter movement with suppositious water. Thus, remaining ostracods stuck to the water surface due to their hydrophobic valve surface characteristic.

A species–area curve is calculated based on the Jaccard-coefficient. Therefore, 20 samples were taken from a species-rich lake in the study area (Lake Kummerower See, Fig. 1: 20), in which 12 different species were identified at that time. To optimize the sampling procedure in terms of treatment, time consumption due to collection in the field, and picking the individuals in the laboratory, we restricted our sampling to eight short cores (total of 182 cm²) at each locality. Following this compromise, approx. 95 % of the expected species were still caught based on limited trials (Fig. 2), and all live samples of one field day could be treated within 48 hours. One exhauster was used for each lake.

In the laboratory, living individuals were sorted and enumerated under a stereo-microscope. Identifications and taxonomy was adopted from Meisch (2000). Single specimens were prepared and the soft parts mounted on microscopic slides in HydroMatrix[®], while the analogous valves were stored in Celka[®]-slides where necessary. All other ostracods were stored in small glass vials filled with 70% ethanol.

Loc.Nr. key	Lake (closest municipality)	Coordinates (Potsdam date)		Mean water depth (m)	Lake area (10 ⁴ m ²)
1	Nonnensee (Bergen)	54° 26′ 00.2″ N	13° 25′ 13.3″ E	1.6	81.8
2	Ossen (Bergen)	54° 26′ 38.8″ N	13° 28' 10.0" E	1.5	34.6
3	Schmachter See (Binz)	54° 24' 02.7" N	13° 35′ 17.7″ E	2.3	119.8
4	Speicher Prohn (Prohn)	54° 23' 00.3" N	13° 02′ 29.0″ E	2.2	58.5
5	Günzer See (Günz)	54° 21′ 44.3″ N	12° 54′ 13.6″ E	1.3	14.7
6	Moorteich (Stralsund)	54° 19′ 01.5″ N	13° 04' 31.9" E	1.9	21.8
7	Garzer See (Garz)	54° 18′ 36.7″ N	13° 20′ 59.6″ E	2.7	15.0
8	Eixener See (Eixen)	54° 10′ 20.5″ N	12° 43′ 42.2″ E	2.2	14.9
9	Cämmerer See (Peenemünde)	54° 08' 06.7" N	13° 47' 03.2" E	2.3	32.4
10	Kölpinsee (Kölpinsee)	54° 02′ 16.1″ N	14° 01' 56.4" E	4.3	27.9
11	Schlosssee Wrangelsburg (Wrangelsburg)	54° 01′ 14.9″ N	13° 36' 08.2" E	2.4	12.4
12	Großer Krebssee (Neu Sallenthin)	53° 57′ 55.2″ N	14° 06' 51.5" E	4.9	38.9
13	Kleiner Krebssee (Neu Sallenthin)	53° 57′ 25.6″ N	14° 06' 45.1" E	4.6	28.2
14	Kosenowsee (Gützkow)	53° 55′ 53.5″ N	13° 25′ 52.6″ E	4.4	16.3
15	Wolgast See (Korswandt)	53° 55′ 13.8″ N	14° 10' 17.7" E	5.1	46.5
16	Großer See Pinnow (Pinnow)	53° 54′ 35.1″ N	13° 48' 21.4" E	6.4	64.4
17	Krebssee (Ulrichshorst)	53° 54′ 16.7″ N	14° 09' 40.5" E	3.9	5.2
18	Klostersee (Dargun)	53° 53′ 53.1″ N	12° 51' 04.0" E	3.9	27.1
19	Usedomer See (Usedom)	53° 51′ 47.1″ N	13° 57' 08.6" E	5.8	370.3
20	Kummerower See (Kummerow)	53° 46′ 34.5″ N	12° 49′ 52.3″ E	9.1	3254.8
21	Großer Siedenbollentiner See (Siedenbollentin)	53° 44′ 10.4″ N	13° 22′ 37.6″ E	5.5	5.7
22	Tüzer See (Tüzen)	53° 43′ 30.9″ N	13° 02′ 11.4″ E	5.6	26.7
23	Ivenacker See (Ivenack)	53° 42′ 47.1″ N	12° 57′ 20.2″ E	2.1	73.3
24	Altwigshagener See (Altwigshagen)	53° 42′ 28.3″ N	13° 49′ 58.4″ E	3.7	15.5
25	Malchiner See (Seedorf)	53° 41′ 42.9″ N	12° 38′ 22.2″ E	3.5	1395.2
26	Kastorfer See (Kastorf)	53° 39′ 15.5″ N	13° 05' 20.9" E	5.2	67.1
27	Rittermannshagener See (Rittermannshagen)	53° 37′ 02.4″ N	12° 45′ 42.0″ E	2.6	62.4
28	Demenzsee (Rosenthal)	53° 33′ 08.1″ N	13° 48' 09.9" E	6.0	13.3
29	Kleiner See bei Koblentz (Koblentz)	53° 31′ 31.2″ N	14° 07' 58.5" E	2.0	21.9
30	Haussee (Rothenklempenow)	53° 30′ 55.4″ N	14° 11' 17.0" E	2.9	34.7
31	Tollensesee (Neubrandenburg)	53° 31′ 47.6″ N	13° 13′ 39.0" E	5.6	1789.6
32	Löcknitzer See (Löcknitz)	53° 26′ 48.5″ N	14° 14' 12.6" E	5.0	44.6
33	Großer Kutzowsee (Plöwen)	53° 28′ 27.3″ N	14° 17′ 50.2″ E	5.7	18

Table 2. Summary of selected environmental data for the investigated lakes which are included in the CCA

Water for analytical purposes was taken at each locality and date close to the sediment surface and before any other sampling procedure. While water temperature (TEMP) (°C; oximeter WTW 'OXI 96'[®]), oxygen (mg dm⁻³; oximeter WTW 'OXI 96'[®]), pH (field lab Aquamerck[®]), conductivity (μ S cm⁻¹; conductometer WTW 'LF 96'[®]), water hardness (CaO mg dm⁻³; field lab Aquamerck[®]), and carbonate hardness (CaO mg dm⁻³; field lab Aquamerck[®]), and carbonate hardness (CaO mg dm⁻³; field lab Aquamerck[®]) were measured in the field, additional water analyses based on standard

methods (DEV, 1989), such as Secchi-visibility, Chlorophyll-a ($\mu g \text{ dm}^{-3}$), NH₄-N (mg dm⁻³), NO₂-N (mg dm⁻³), NO₃-N (mg dm⁻³), total N (mg dm⁻³), oPO₄-P (mg dm⁻³), total P (mg dm⁻³), Cl (mg dm⁻³), Ca (mg dm⁻³), and Mg (mg dm⁻³) were done by the analytical laboratory of the State Office of Environment, Nature Conservation and Geology (LUNG-MV), Güstrow, Germany. Furthermore, the morphological parameters of the lake basins such as: maximum depth, mean depth, lake area, lake volume, and catchment were



Figure 2. Species-area curve (Jaccard-coefficient) with calculated similarity distances between samples.

accessible through the State Department of Environment of Mecklenburg-Vorpommern (UM-MV), Schwerin, Germany (Mathes et al. unpubl.).

Numerical analysis

Data screening

Prior to the final statistical analysis, the species and environmental data were screened to identify and eliminate redundant environmental variables, unusual or 'outlier' samples, and environmental variables that do not appear to determine ostracod distributions (ter Braak & Šmilauer, 2002). The distribution of the environmental data was positively skewed and therefore log-transformed (log x + 5) to fit normal distribution. The morphological and environmental variables were tested for correlation (p < 0.01). In addition, all variables showed high collinearity were deleted, as assessed by variance inflation factors > 10 in an exploratory detrended correspondence analysis (DCA) of the complete environmental dataset in which all variables were regressed onto the DCA axes (ter Braak, 1987).

To take ostracod phenology into further account, data were only used for statistical analysis when adult and A-1 -instars were collected simultaneously at one locality, to assure molt activity and so the ecological optimum of a species.

To eliminate rare species from the calibration dataset, only species present in at least three different localities were considered. Finally, the sample species scores were standardized by the sample percentage.

Data Analysis

Multivariate statistics were performed with the computer software CANOCO (ter Braak & Šmilauer, 2002). Prior to analysis, each variable was tested on collinearity. A canonical correspondence analysis (CCA) was used to investigate the relationships between modern ostracod assemblages and associated environmental variables from the calibration dataset. Forward selection and Monte Carlo permutation tests (499 unrestricted permutations, p < 0.01) were used to classify and identify a subset of environmental variables, which describe almost as much variation in the ostracod species assemblages as the entire environmental dataset.

Weighted averaging regression

Weighted averaging (WA) models are commonly used in paleoecology to establish robust transfer functions for potential organism groups (e.g., foraminifers, diatoms, chironomids (Imbrie & Kipp, 1971, Pienitz et al., 1995, Lotter et al., 1999). WA regression is used to estimate the optimum and tolerance for each taxon from the calibration dataset (ter Braak & Looman, 1986).

The present WA model was calculated with the computer software C^2 (Juggins, 2003). Finally, the model was applied to a previously published Quaternary ostracod dataset of Lake Krakower See (Viehberg, 2004).

Results

Out of 116 sampling dates 47 ostracod species were identified (See Electronic Supplementary Material¹). *Candonopsis scourfieldi* and *Pseudocandona sucki* were documented new for the first time in the study area, while nine species were rediscovered in the study area 100 years after the last published record (according to Frenzel & Viehberg, 2004): *Bradleystrandesia reticulata, Cypria exsculpta, Cyprois marginata, Eucypris virens, Fabaeformiscandona balatonica, F. holzkampfi, F. hyalina, Pseudocandona insculpta,* and *P. marchica.* Some common species are among the list of rediscovered species, because routine freshwater monitoring programs focus mainly on planktonic organisms or macrozoobenthos (LUNG M-V, 2001; UM-MV,

¹ Electronic Supplementary Material is available for the article at http://www.dx.doi.org/10.1007/s10750-006-0241-x.

1998), and investigations focused on ostracods or meiobenthos are rare (e.g., Hollwedel & Scharf, 1994, 1996; Viehberg, 2001).

Multivariate Statistics

Following the data-screening procedures, as outlined above, it became apparent that the investigated lakes were morphologically similar (p < 0.01). The parameter 'lake area' was selected for further calculations as it was least correlated to Other environmental variables. eliminated parameters were total N, total P, Chlorophyll-a, conductivity, and total water hardness because they either showed significant correlation (p < 0.01) to more than two other variables and/or had a high variance inflation factor in an exploratory DCA (not shown here). A Pearson correlation matrix showed the collinearity of the remaining parameters (Table 3).

The final calibration dataset for further analysis consisted of 72 samples, 31 species, and 13 environmental variables (i.e., lake area, TEMP, oxygen, pH, carbonate water hardness, Secchi-visibility, NH₄-N, NO₂-N, NO₃-N, oPO₄-P, Ca, Mg, Cl).

CCA

The eigenvalues for CCA axis 1 (0.21) and axis 2 (0.14) explain 11.3 % of the cumulative variance in the weighted averages of the ostracod taxa. The high ostracod-environment correlations obtained

for CCA axis 1 (0.82) and axis (0.74), indicate a high (p < 0.01) relationship between the ostracod taxa and the selected environmental parameters.

Using forward selection with Monte Carlo permutation tests, CCA identified four environmental variables (TEMP, Mg, Ca, and lake area) that significantly explained the variation in the ostracod assemblages. This set of variables accounted for 14.7% of the variance (TEMP 6.1%, Mg 3.7%, Ca 2.6%, and lake area 2.3%) (Fig. 3).

The CCA biplot clearly illustrated that TEMP best explains ostracod species variation, and two groups of species can be distinguished. One group of early year forms cluster on the right-hand side of the biplot, while the other species found in the left quadrants are positively correlated to TEMP. Beside thermal aspects, the occurrence of *Cyprideis torosa*, *F. holzkampfi*, *F. fragilis*, and *Potamocypris unicaudata* were affected by increased Mg-levels. Individuals of *Candona neglecta* were additionally influenced by lake area.

WA models for paleotemperature reconstructions

TEMP was selected as the environmental variable for the WA model (Birks, 1995). The residuals showed a significant trend ($r^2 = 0.26$; p < 0.01) with inverse deshrinking regression and no trend ($r^2 < 0.001$; p < 0.01) with classical deshrinking regression (Fig. 4 & 5). The latter was therefore used for further calculations, despite the higher

Table 3. Pearson correlation matrix shows the correlation among the considered environmental variables

	Area	Temp	pН	dCH	O ₂	NH ₄ -N	NO ₂ -N	NO ₃ -N	oPO ₄ -P	Ca	Mg	Cl
Secchi	0.31**	-0.21	-0.15	-0.07	0.08	-0.15	-0.12	0.00	-0.07	-0.13	-0.09	-0.19
Area		-0.04	0.11	0.08	0.09	-0.15	0.06	0.13	-0.12	0.13	0.04	-0.08
Temp			0.51**	0.10	-0.31^{*}	-0.03	0.06	-0.13	0.23	-0.07	-0.01	0.03
pН				0.13	0.07	-0.24	0.02	-0.10	0.14	0.15	0.25	0.25
dCH					-0.01	-0.15	0.26	0.27	0.13	0.68^{**}	0.49^{**}	0.21
O_2						-0.29^{*}	0.10	0.18	-0.29	-0.08	-0.05	-0.14
NH ₄ -N							0.22	0.15	0.33^{*}	-0.02	-0.29	-0.27
NO ₂ -N								0.78^{**}	0.06	0.26	0.07	-0.09
NO ₃ -N									-0.10	0.27	0.05	-0.16
oPO ₄ -P										0.05	0.01	-0.08
Ca											0.53^{**}	0.16
Mg												0.66***

* and ** represent 0.01 and 0.001 significant levels. n = 72.



Figure 3 Canonical correspondence analysis of the screened calibration dataset (n = 72 samples; species code see Electronic Supplementary Material).

RMSE (3.66), as it provides the more reliable inferences of lake TEMP.

Optima and tolerances were estimated for those ostracods that do not produce new generations over the year continuously (Table 4).

Applying WA Model to Lake Krakower See

Lake Krakower See (16 km², \sim 28 m max depth) is situated in central Mecklenburg-Vorpommern and has been subject to other paleolimnological investigations prior (Fig. 1; e.g. Lorenz 2002; Viehberg, 2004). The WA model was applied to infer past lake water temperature for Lake Krakower See. A dataset of the subfossil ostracod assemblage from a Holocene/Pleistocene core (KOS III) was previously described and used for water level reconstructions (Viehberg, 2004). For further interpreting the ostracod-inferred temperature (OIT) model was split into a 'non-summer' (Fig. 6; (a)) and 'summer' (Fig. 6; (b)) aspect. The first graph is based on species which do not mature in summer. It varies between 4.5 °C and 6.5 °C over the investigated time span. A larger amplitude and apparently higher TEMP (14.7 to 21.1 °C) was calculated by an approximation, which is exclusively based on ostracod maturing in summer (Fig.6; (b)). The full OIT model estimated TEMP between 4.5 °C and 11.7 °C (Fig.6; (c)). Nevertheless, the different curves showed similar trends. In the pollen zone VI a rise of the water TEMP was estimated followed by a drop in pollen zone VII. Throughout the following pollen zone the water temperature was stabile or slightly increasing. In pollen zone III the ostracod record did not hold any species, which were included in the presented WA-model. Similarly, pollen zone VII does not contain species, which were considered in the 'summer'-aspect.

Discussion

In recent years, transfer functions have greatly improved the results of paleoecological recon-



Figure 4. Performance of the WA-Model (inverse deshrinking). Plots of observed versus ostracod-inferred temperature and observed minus ostracod inferred temperature and calibration models using inverse deshrinking.

structions from description-oriented studies to a more exact science with the capacity to provide precise quantitative data on environmental change. However, these statistical methods have to be used with care in paleontological records. It still remains necessary to analyze the assemblages on autochthonous and allochthonous aspects based on general ecological knowledge, to assure that applications of statistical models are justified (Boomer et al., 2003). From the model point of



Figure 5. Performance of the WA-Model (classical deshrinking). Plots of observed versus ostracod-inferred temperature and observed minus ostracod inferred temperature and calibration models using classical deshrinking.

view, it is essential to monitor the phenology of ostracods in order to document their ecological needs, because strong calibration datasets are based on the ecological optimum of a species. For ostracods, the ecological optimum is assumed to exist at the time of final molting and subsequent reproduction (De Deckker, 2002). The compiled and presented calibration dataset follows the phenology of each ostracod species. It

Table 4. (WA) Estimated optima. Maximum relative abundance, number of occurrences, WA optima of ostracod species, and tolerance.

Species name	Max. abund.	Num. occur.	Temp [°C]	Tolerance [°C]
Candona candida	0.48	24	7.2	1.9
Candona neglecta	0.54	9	7.6	2.2
Candona weltneri	0.47	10	6.0	2.4
Candonopsis kingsleii	0.23	7	9.3	3.6
Candonopsis scourfieldi	0.11	5	6.6	1.9
Cyclocypris serena	0.30	4	6.7	4.6
Fabaeformiscandona fabaeformis	0.30	6	7.6	2.2
Fabaeformiscandona fragilis	0.61	6	7.6	2.8
Fabaeformiscandona holzkampfi	0.53	5	10.7	1.2
Fabaeformiscandona hyalina	0.54	5	8.0	2.2
Fabaeformiscandona levanderi	0.35	9	10.1	5.2
Fabaeformiscandona protzi	0.54	11	6.2	2.9
Herpetocypris chevreuxi	0.73	4	20.3	5.4
Ilyocypris decipiens	0.59	7	17.1	3.2
Metacypris cordata	0.27	5	16.2	6.7
Notodromas monacha	0.31	5	21.4	1.5
Physocypria kraepelini	0.13	3	20.0	0.6
Plesiocypridopsis newtoni	0.58	8	20.8	1.7
Potamocypris unicaudata	0.71	7	17.2	5.1
Pseudocandona compressa	0.70	31	13.5	5.6
Pseudocandona insculpta	0.32	11	14.9	5.2
Pseudocandona marchica	0.35	7	12.5	4.5

does not take the broad lifespan tolerance into further account, as this would weaken the model. For example, Candona candida, which is described as an early year form (Meisch, 2000), was found in a temperature range of +1.6 to 23.5 °C (dataset of this study) and reveals a thermoplastic behavior. The inferred WA-optimum (7.2 °C) corresponds to the fact that the species reaches maturity and reproduces in colder conditions. The opposite can be observed for *Ilvocypris* decipiens. This species reproduces in summer and although it tolerates colder temperature values (+1.6 °C; dataset of this study), the calculated optimum is 17.1 °C. Thus, the transfer function quantifies the descriptive approximation known from literature.

Canonical analyses of the presented calibration dataset revealed TEMP as the main environmental variable, which controls ostracod distribution in the studied lakes. Likewise, it has been shown in laboratory studies that TEMP influences the reproduction, growth rate, size, and life span of ostracods (e.g., Ganning, 1971; Martens et al., 1985). Anyway, the selection of the localities in the study area might not represent a sufficient gradient for other variables to be shown in ostracod abundances. This might also be the reason for the lacking overall performance of the quantitative model. In this context, it is regrettable that published ecological data of extensive field work in adjacent areas (e.g., Hiller, 1972; Sywula, 1974; Vesper, 1975) cannot be integrated to the existing dataset, as the transformed and often descriptive results are not suitable for use in quantitative models. But even in modern ecological investigations (e.g., Rossetti et al., 2004, Yilmaz & Külköylüoglu, 2006), the species optima and tolerances were calculated regardless of the maturing period and so they can only be applied with restriction to ecological reconstructions.

The appliance of the ostracod-inference model (OIT) to an exemplary ostracod assemblage seems reasonable. It shows an overall trend of increasing



Figure 6. Ostracod-inferred temperature (OIT) model. Ostracod record of core KOS II from Lake Krakower See (Viehberg 2004); (a) OIT based on non-summer species, (b) OIT based on summer species, (c) OIT based on all species in the presented calibration dataset.

water temperature through the Holocene in Lake Krakower See. However, these estimates have to be interpreted not only in terms of climate change but also by hydrological variations, which had the potential to overrule climate signals (see Lorenz, 2002). During low water conditions (pollen zone VI) the inferred water TEMP was warmer, while high water level conditions (pollen zone II and VII) corresponded to colder TEMP estimates. In this context, it is noteworthy that 'summer species' were absent at some intervals and were never found exclusively in any samples. Whereas in some samples species with colder tolerances are present exclusively, so cold seasonal environments occurred at all times. This fact can be explained by shifts in hydrological and/or climate regime, which hindered the development of thermophile species. The results of the present model are reasonable and support the understanding of the lake evolution of Lake Krakower See. At present, there are no other quantitative lake water temperature reconstructions in the study area.

Conclusion

A first ostracod calibration dataset for northeast Europe is presented here. It is based on a continuous monitor program throughout the year, which only recorded the environmental variables at the time of the final species-specific molt period. The freshwater ostracod species in the presented study were most significantly correlated to water temperature in accordance to a canonical correspondence analyses. A weighted averaging model was set up to use subfossil ostracod assemblages from Lake Krakower See to quantify past water temperature. The model supports the proposed hydrological changes in Late Pleistocene and Holocene based on sedimentary records. Inferred colder periods match high water level and vice versa. It is the first lake water temperature reconstruction in this area.

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References

- Alin, S. R. & A. S. Cohen, 2003. Lake-level history of Lake Tanganyika, East Africa, for the past 2500 years based on ostracode-inferred water-depth reconstruction. Palaeogeography Palaeoclimatology Palaeoecology 199: 31–49.
- Birks, H. J. B., 1995. Quantitative palaeoenvironmental reconstructions. In Maddy, D. & J. S. Brew (eds), Statistical

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modelling of Quaternary science data, 5. Quaternary Research Association, Cambridge, 161–254.

- Boomer, I., D. J. Horne & I. J. Slipper, 2003. The use of ostracods in Palaeoenvironmental studies, or what can you do with an ostracod shell? Paleontological Society Papers 9: 153–180.
- Boomer, I., R. Whatley & N. V. Aladin, 1996. Aral Sea Ostracoda as environmental indicators. Lethaia 29: 77–85.
- Colman, S. M., R. M. Forester, R. L. Reynolds, D. S. Sweetkind, J. W. King, P. Gangemi, G. A. Jones, L. D. Keigwin & D. S. Foster, 1994. Lake-level history of Lake Michigan for the past 12,000 years: The record from deep lacustrine sediments. Journal of Great Lakes Research 20: 73–92.
- Colman, S. M., G. A. Jones, R. M. Forester & D. S. Foster, 1990. Holocene paleoclimatic evidence and sedimentation rates from a core in southwestern Lake Michigan (USA). Journal of Paleolimnology 4: 269–283.
- De Deckker, P., 2002. Ostracod palaeoecology. In Holmes, J. A. & A. R. Chivas (eds), The ostracoda: applications in Quaternary research, 131. American Geophysical Union, Washington, DC, 121–134.
- DEV, 1989. Deutsche Einheitsverfahren zur Wasser-, Abwasser- und Schlammuntersuchung. Verlag Chemie, Weinheim.
- Duphorn K., Kliewe H., Niedermeyer R. -O., Janke W., Werner F., 1995. Die deutsche Ostseeküste. In: Sammlung Geologischer Führer, vol. 88, Bornträger, Berlin, Stuttgart, pp 281.
- Forester, R. M., 1991. Ostracode assemblages from springs in the western USA: Implications for paleohydrology. Memoirs Of The Entomological Society Of Canada 155: 181–202.
- Frenzel, P. & F. A. Viehberg, 2004. Checklist of Recent und Quaternary ostracods (Crustacea) from freshwater, brackish and marine environments in Mecklenburg-Vorpommern, NE-Germany. Revista Española de Micropaleontologia 36: 29–55.
- Ganning, B., 1971. On the ecology of *Heterocypris salinus*, *H. incongruens and Cypridopsis aculeata* (Crustacea : Ostracoda) from Baltic brackish-water rockpools. Marine Biology. International Journal on Life in Oceans and Coastal Waters 8: 271–279.
- Gell, P. A., P. A. Barker, P. De Deckker, W. M. Last & L. Jelicic, 1994. The Holocene history of West Basin lake, Victoria, Australia: chemical changes based on fossil biota and sediment mineralogy. Journal of Paleolimnology 12: 235–258.
- Hiller, D., 1972. Untersuchungen zur Biologie und zur Ökologie limnischer Ostracoden aus der Umgebung von Hamburg. Archiv für Hydrobiologie 40: 400–497.
- Hollwedel, W. & B. W. Scharf, 1994. Zur Verbreitung der Cladoceren und Ostracoden auf den Ostseeinseln Rügen und Hiddensee. Drosera, Oldenburg 1994: 21–28.
- Hollwedel, W. & B. W. Scharf, 1996. Zur Verbreitung der Cladoceren und Ostracoden (Crustacea) in Gewässern des Müritz-Nationalparks (Mecklenburg-Vorpommern). Braunschweiger Naturkundliche Schriften 5: 91–104.
- Holmes, J. A., 2003. Future trends and goals in ostracode research. Paleontological Society Papers 9: 275–290.
- Holmes, J. A. & A. R. Chivas, 2002. Ostracod shell chemistryoverview. In Holmes, J. A. & A. R. Chivas (eds), The

Ostracoda: applications in Quaternary research, 131. American Geophysical Union, Washington, DC, 185–204.

- Imbrie, J. & N. G. Kipp, 1971. A new micropaleontological method for quantitative paleoclimatology: application to a late Pleistocene Caribbean core. In Turekian, K. K. (ed.), The Late Cenozoic glacial ages. Yale University Press, New Haven, CT, 71–181.
- Juggins, S., 2003. Tutorial C²: software for ecological and palaeoecological data analysis and visualisation. University of Newcastle, Newcastle upon Tyne, UK.
- Kaiser, K., 2001. Die spätpleistozäne bis frühholozäne Beckenentwicklung in Mecklenburg-Vorpommern. Greifswalder Geographische Arbeiten 24: 1–259.
- Külköylüoglu, O. & M. Dügel, 2004. Ecology and spatiotemporal patterns of Ostracoda (Crustacea) from Lake Golcuk (Bolu, Turkey). Archiv für Hydrobiologie 160: 67–83.
- Lorenz S., 2002. Die Uferstrukturen des Krakower Sees in Mecklenburg – Naturräumliche Analyse und jungquartäre Paläohydrologie. Diploma thesis, University of Greifswald, Greifswald, Germany.
- Lotter, A. F., I. R. Walker, S. J. Brooks & W. Hofmann, 1999. An intercontinental comparison of chironomid palaeotemperature interference models: Europe vs. North America. Quaternary Science Reviews 18: 717–735.
- LUNG M-V, 2001. Gewässergütebericht Mecklenburg-Vorpommern 1998/1999: Ergebnisse der Güteüberwachung der Fließ-, Stand- und Küstengewässer und des Grundwassers in Mecklenburg-Vorpommern. Landesamt für Umwelt, Naturschutz und Geologie Mecklenburg-Vorpommern, Güstrow.
- Martens, K., P. DeDeckker & T. G. Marples, 1985. Life history of *Mytiolocypris henricae* Chapman. Crustacea: Ostracoda. Australian Journal of Marine and Freshwater Research 36: 807–819.
- Meisch, C., 2000. Freshwater Ostracoda of Western and Central Europe. In Schwoerbel, J. & P. Zwick (eds), Süßwasserfauna von Mitteleuropa, vol. 8/3. Akademischer Verlag Spektrum, Heidelberg, 522.
- Mourguiart, P., T. Correge, D. Wirrmann, J. Argollo, M. E. Montenegro, M. Pourchet & P. Carbonel, 1998. Holocene palaeohydrology of Lake Titicaca estimated from an ostracod-based transfer function. Palaeogeography Palaeoclimatology Palaeoecology 143: 51–72.
- Müller, O. F., 1772. Observations on some bivalved insects, found in common water, by Mr Mueller, of the Academy of Sciences in Bavaria and the Oeconomical Society at Bern (Communicated by R.H.A. Bennet, Esq.). Philosophical Transactions Of The Royal Society Of London 61: 230–246.
- Müller, U., N. Rühberg & H.-D. Krienke, 1995. The Pleistocene sequence in Mecklenburg-Vorpommern. In Ehlers, J., S. Kozarski & P. Gibbard (eds), Glacial deposits in North-East Europe. A.A. Balkema, Rotterdam, 501–516.
- Namiotko, T., B. Wisniewska & A. Milosek, 1993. Changes of Lake Hancza (NE Poland) ecological state in the last fifty years with particular attention being paid to the profundal ostracoda fauna. Polskie Archiwum Hydrobiologii 40: 267–290.

- Pienitz, R., J. P. Smol & H. J. B. Birks, 1995. Assessment of freshwater diatoms as quantitative indicators of past climatic change in the Yukon and Northwest Territories, Canada. Journal of Paleolimnology 13: 21–49.
- Redeke, H. C., 1936. Flora und Fauna der Zuidersee. Monografie van een Brakwatergebied, Den Helder.
- Rossetti, G., M. Bartoli & K. Martens, 2004. Limnological characteristics and recent ostracods (Crustacea, Ostracoda) of freshwater wetlands in the Parco Oglio Sud (Northern Italy). Annales Limnologie - International Journal of Limnology 40: 329–341.
- Scharf, B. W., 1998. Eutrophication history of lake Arendsee (Germany). Palaeogeography Palaeoclimatology Palaeoecology 140: 85–96.
- Schwalb, A., 2003. Lacustrine ostracodes as stable isotope recorders of late-glacial and Holocene environmental dynamics and climate. Journal of Paleolimnology 29: 267– 351.
- Smith, A. J., Delorme L. D., Forester R. M., 1992. A lake's solute history from ostracodes: Comparison of methods. In: Maest Kharaka (eds), Low temperature environments 677– 680.
- Sywula, T., 1974: Malzoraczki (Ostracoda). In: Fauna Slodkowodna Polski, vol. 24, Panstwowe Wydawnictwo Naukowe, Poznan, 315 pp.
- ter Braak, C. J. F., 1987. Ordination. In: Jongman R. H. G., ter Braak C. J. F., van Tongeren O. F. R. (eds) Data analysis in community and landscape ecology Cambridge University Press, Pudoc, Wageningen, pp 91–290.
- ter Braak, C. J. F. & C. W. N. Looman, 1986. Weighted averaging, logistic regression and the Gaussian response model. Vegetatio 65: 3–11.
- ter Braak, C. J. F. & P. Šmilauer, 2002. CANOCO Reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca, NY.
- UM-MV, 1998. Gewässergütebericht Mecklenburg-Vorpommern 1996/1997: Zustand der Gewässergüte von Fließ-, Standund Küstengewäsern und der Grundwasserbeschaffenheit in Mecklenburg-Vorpommern. Vol. 7, Umweltministerium Mecklenburg-Vorpommern, Schwerin.
- Vesper, B., 1975. Ein Beitrag zur Ostracodenfauna Schleswig-Holsteins. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 72: 97–108.
- Viehberg, F. A., 2001. Neue Erkenntnisse zur Ostrakodenfauna (Crustacea) von Greifswald und Umgebung. Naturschutzarbeit in Mecklenburg-Vorpommern 44: 57–60.
- Viehberg, F. A., 2002. A new and simple method for qualitative sampling of meiobenthos-communities. Limnologica 32: 350–351.
- Viehberg, F. A., 2004. Paleolimnological study based on ostracods (Crustacea) in Late-glacial and Holocene deposits of Lake Krakower See in Mecklenburg-Vorpommern, NE Germany. Studia Quaternaria 21: 109–115.
- Yilmaz, F. & O. Külköylüoglu, 2006. Tolerance, optimum ranges, and ecological requirements of freshwater Ostracoda (Crustacea) in Lake Aladag (Bolu, Turkey). Ecological Research 21: 165–173.