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RESEARCH/REVIEW ARTICLE

Freshwater ostracods (Crustacea) and environmental variability of polygon ponds in the tundra of the Indigirka Lowland, north-east Siberia

Andrea Schneider,[1,2] Sebastian Wetterich,[3] Lutz Schirrmeister,[3] Ulrike Herzschuh,[3,4] Hanno Meyer[3] &
Lyudmila A. Pestryakova[5]

[1] Centre for Arctic Gas Hydrate, Environment and Climate, Department of Geology, University of Tromsø, Dramsveien 201, NO-9037 Tromsø, Norway
[2] Department of Physical Geography and Quaternary Geology, Stockholm University, SE-106 91 Stockholm, Sweden
[3] Department of Periglacial Research, Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Telegrafenberg A43, DE-14473 Potsdam, Germany
[4] Institute of Earth and Environmental Science, Potsdam University of Potsdam, Karl-Liebknecht-Str. 24-25, DE-14476 Potsdam, Germany
[5] Department for Geography and Biology, North Eastern Federal University Yakutsk, ul. Belinskogo 58, RU-677000 Yakutsk, Russia

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Correspondence
Andrea Schneider, Centre for Arctic Gas Hydrate, Environment and Climate, Department of Geology, University of Tromsø, Dramsveien 201, NO-9037 Tromsø, Norway.
E-mail: andrea.schneider@uit.no

Abstract

Freshwater ostracods (Crustacea, Ostracoda) are valuable biological indicators. In Arctic environments, their habitat conditions are barely known and the abundance and diversity of ostracods is documented only in scattered records with incomplete ecological characterization. To determine the taxonomic range of ostracod assemblages and their habitat conditions in polygon ponds in the Indigirka Lowland, north-east Siberia, we collected more than 100 living ostracod individuals per site with a plankton net (mesh size 65 µm) and an exhaustor system from 27 water bodies and studied them in the context of substrate and hydrochemical data. During the summer of 2011, a single pond site and its ostracod population was selected for special study. This first record of the ostracod fauna in the Indigirka Lowland comprises eight species and three additional taxa. *Fabaeformiscandona krochini* and *F. groenlandica* were documented for the first time in continental Siberia. Repeated sampling of a low-centre polygon pond yielded insights into the population dynamics of *F. pedata*. We identified air temperature and precipitation as the main external drivers of water temperatures, water levels, ion concentrations and water stable isotope composition on diurnal and seasonal scales.

To access the supplementary material for this article, please see the supplementary files under Article Tools online.

Ostracods (Arthropoda: Crustacea, Ostracoda) are small crustaceans, mostly 0.1–5 mm long (Meisch 2000), that live in almost all aquatic habitats. Their bivalve shell, consisting of two dorsally connected calcite valves that completely envelope the body, is replaced during successive moulting as ostracods grow to adulthood. Ostracods have a complex soft body with typically eight pairs of appendages performing functions that include locomotion, sensing, feeding, cleaning and mating (Meisch 2000; Horne et al. 2002; Smith & Delorme 2010; Karanovic 2012). The specific morphology of the limbs is used for taxonomic identification. Close to 2000 species of freshwater ostracods are known (Martens et al. 2008), of which 48 species occur in Arctic freshwater bodies (Hodkinson et al. 2013). Seasonal life cycles in combination with freezing- and desiccation-resistant eggs (Smith & Delorme 2010; Karanovic 2012) allow ostracods to colonize temporary habitats that may dry out during summer or are frozen solid during winter. Hence, shallow polygon ponds in the circumpolar Arctic provide a

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Abbreviations in this article
EC: Electrical conductivity
TC: Total carbon
TIC: Total inorganic carbon
TN: Total nitrogen
TOC: Total organic carbon
TS: Total sulfur

suitable, but rarely studied, habitat for freshwater ostracods.

Freshwater ostracods are sensitive to environmental conditions in their habitat. A key advantage of ostracods as biological indicators is that they have been present in aquatic environments since the Palaeozoic era and therefore present the most complete fossil record of any extant arthropod group (Moore 1961). Abundant and well preserved in lacustrine sediments, ostracod valves provide an excellent microfossil record (e.g., Delorme 1969, 1989; Holmes & Chivas 2002; Holmes 2003). Hence, freshwater ostracods are of great interest as biological indicators of climate and environmental changes in the Quaternary past and in modern studies (e.g., Holmes 1992; Holmes & Chivas 2002; Horne et al. 2012).

Ice-wedge polygons form in cold-climate environments under permafrost conditions and are the most common periglacial patterned ground features in the circumpolar Arctic (Fig. 1). Modern ice-wedge polygon landscapes are estimated to cover from 250 000 km^2 (Minke et al. 2007) to 400 000 km^2 (Muster et al. 2013) in circumarctic coastal lowlands. Due to cold and dry winter conditions, freeze–thaw cycles in the ground form a periglacial microrelief with frost cracks, ice wedges and polygons. The permafrost and its surficial polygon microrelief block drainage, allowing ponding in numerous small depressions. According to Meyer (2003), different types of freshwater bodies form depending upon the stage of polygon development or degradation. Periglacial water bodies are the most abundant aquatic ecosystem type in the Arctic (Grosse et al. 2013) and are hotspots of biological activity in the otherwise hostile tundra, providing diverse habitats for microbes, plants, birds and aquatic communities (e.g., Vincent et al. 2008; Bobrov et al. 2013), including freshwater ostracods (e.g., Wetterich, Herzschuh et al. 2008; Wetterich, Schirrmeister et al. 2008; Bunbury & Gajewski 2009). Substrate from fossilized polygon ponds contains well-preserved biological remains, providing excellent natural archives in areas where other archives are rare or absent. A number of late Quaternary environmental reconstructions from permafrost areas of north-eastern Siberia use a multi-proxy approach, combining various biological indicators from fossil deposits (Schirrmeister et al. 2002; Kienast et al. 2008; Andreev et al. 2011; Schirrmeister 2011). Freshwater ostracods provide critical information that enables us to reconstruct a complex picture of climate and permafrost landscape dynamics throughout the late Quaternary past (Wetterich et al. 2005; Wetterich, Kuzmina et al. 2008; Wetterich et al. 2009; Kienast et al. 2011).

Reference data sets on species assemblages and instrumental records of environmental parameters are required to precisely evaluate ostracod records from permafrost areas. Modern ostracod fauna and their ecology in the mid-latitudes of Europe (e.g., Meisch 2000; Kempf 2006; Viehberg 2006; Horne 2007; Decrouy et al. 2011; Poquet & Mesquita-Joanes 2011) and northern America (e.g., Delorme 1969, 1989, 1991; Smith 1993; Curry 1999; Smith & Delorme 2010) are relatively well known. In contrast, basic knowledge about recent ostracod abundance, diversity, life cycles and ecology in sub-Arctic and Arctic permafrost habitats is limited to small areas (e.g., Alm 1914, 1915; Pietrzeniuk 1977; Semenova 2003; Bunbury & Gajewski 2005, 2009; Wetterich, Schirrmeister et al. 2008) or is lacking entirely for many regions. This gap in ostracod data fundamentally limits their use as biological indicators in high-latitude areas, where the effects of climatic change are expected to be the strongest (Symon et al. 2005; Prowse et al. 2006; Stocker et al. 2013).

Within the joint German–Russian project Polygons in Tundra Wetlands: State and Dynamics under Climate Variability in Polar Regions, field studies of recent environmental dynamics in polygon ponds were carried out in the Indigirka Lowland of north-east Siberia in summer 2011 (Schirrmeister et al. 2012). The study presented here aimed to (1) conduct an inventory of the abundance, diversity and ecological ranges of the living ostracod assemblages, (2) determine present-day baseline characteristics of polygon ponds in the Indigirka Lowland and (3) detect temporal variability in a polygon pond during the Arctic summer season.

Study site

The field studies were carried out in the vicinity of the Kytalyk World Wildlife Fund field station located 28 km north-west of the settlement of Chokurdakh (70°83′12.1″N, 147°48′29.9″E, elevation 11 m a.s.l.) in the Indigirka Lowland in north-east Siberia, Russia (Fig. 1). The vegetation in the study area is classified as dwarf shrub, tussock-sedge and moss tundra (CAVM Team 2003). Detailed vegetation records of the study area are summarized in Supplementary Table S1. The climate is continental, with high annual temperature gradients and low precipitation. The closest meteorological station in Chokurdakh (World Meteorological Organization station

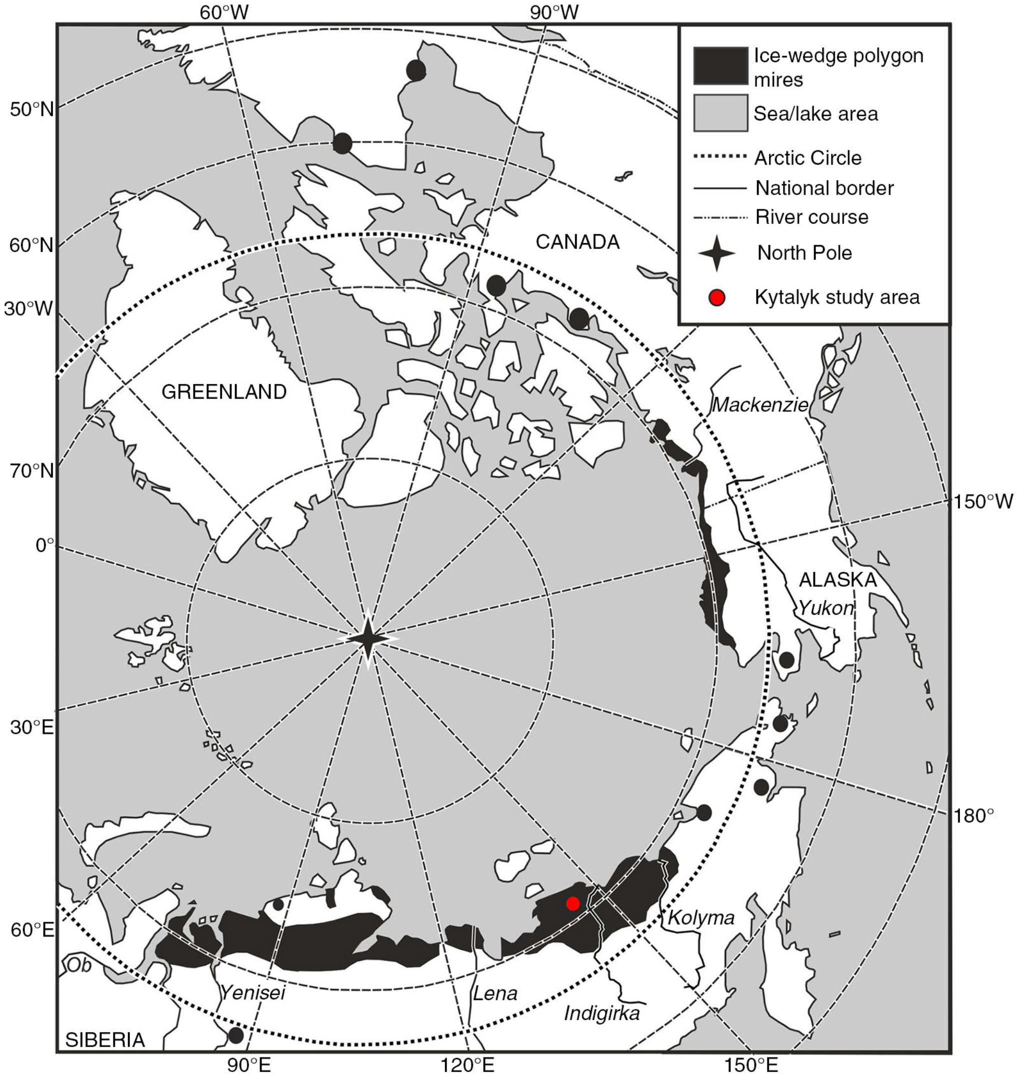

Fig. 1 Distribution of polygon landscapes in the Arctic. The study area near the World Wildlife Fund Kytalyk field station in the north-east Siberian Indigirka Lowland is indicated by a red marker. Map kindly provided by Pim de Klerk (Freie Universität Berlin and State Museum of Natural History in Karlsruhe, Germany) and modified after Minke et al. (2007).

no. 21946) recorded +9.7°C as the mean temperature of the warmest month (T_{July}) and −36.6°C as the mean temperature of the coldest month ($T_{January}$). The mean annual air temperature (T_{Ann}) is −14.2°C and the mean annual precipitation (P_{Ann}) is 354 mm (Rivas-Martínez 1996–2009). The region is underlain by continuous permafrost (Eršov 1991) that formed throughout the Quaternary past and is maintained by the current climate conditions; only the uppermost ground layer thaws seasonally. The permafrost is 200–300 m thick; its temperature ranges from below −10°C (Tumel 2002) to a temperature range between −6 and −4°C (Eršov 1991).

The Berelekh River floodplain and the adjacent thermokarst-affected lowland represent the major landscape units in the study area (Fig. 2). The 4–7 km wide Berelekh River valley allows the river to meander. River course shifting and water level fluctuations expose bare or sparsely vegetated fluvial sediments to freezing air temperatures, creating frost crack systems. In the tundra lowland, 20–30 m high ridges of late Pleistocene-aged Ice Complex deposits (Lavrušin 1963; Kaplina et al. 1980) occur as remains of formerly widespread ice-rich permafrost. After its degradation in response to Lateglacial and Holocene climate warming, permafrost thaw and ground subsidence (thermokarst) resulted in the formation of circular depressions with diameters of several kilometres (alas; Czudek & Demek 1970) alternating with remnant ridges of Ice Complex deposits (yedoma;

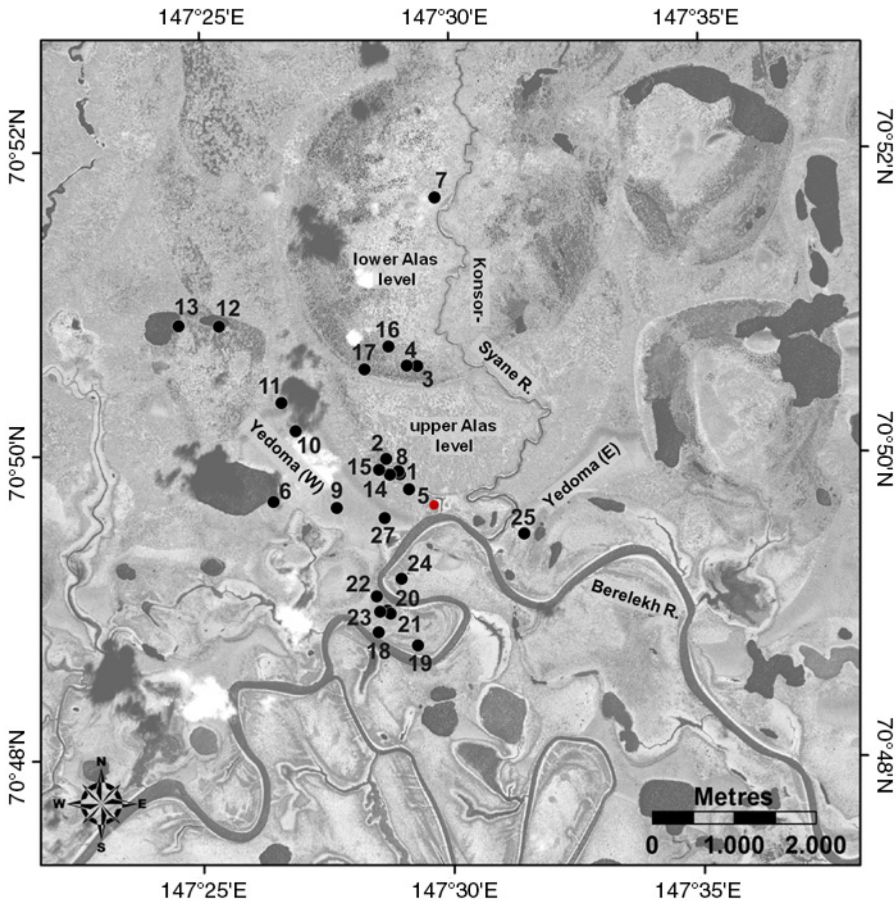

Fig. 2 The study area around the Kytalyk field station (red marker) includes several yedoma ridges, alas depressions located between the western (W) and eastern (E) yedoma ridge, and the Berelekh River floodplain as shown in a panchromatic/multi-spectral imagery satellite image from August 2010 with 0.5 m resolution (GeoEye 4318026). The numbers indicate the pond locations. Courtesy of J. van Huissteden (Vrije Universiteit Amsterdam, Faculty of Earth and Life Sciences, The Netherlands). Map compiled by Mathias Ulrich (Leipzig University, Germany).

Schirrmeister et al. 2013). Alas depressions are often occupied by lakes or, after lake drainage events, by peatlands. On the bottom of drained thermokarst lakes, frost cracking and ice-wedge polygons are common (Mackay 2000). The alas to be found north of the Kytalyk field station is located between two yedoma ridges. It has a diameter of 5.5 km and is drained by the Konsor Syane River, a tributary of the Berelekh River (Fig. 2). Two levels, differing in height by 1–1.5 m located 4–6 m above the Berelekh River level, were distinguished. Ice-wedge polygons occupy both alas depressions and the Berelekh River floodplain but are rare on the yedoma.

At an initial stage of development the centre of individual low-centre polygons forms a depression (intrapolygon) that is often filled by water (Supplementary Fig. S1, Kyt-04-16). During ongoing sedimentation, peat accumulation or permafrost degradation, interpolygon ponds (Supplementary Fig. S1, Fig. 3, Kyt-14-18-22) can form along the frost crack directly above thawing ice wedges. Further permafrost degradation leads to the formation of thaw lakes which continuously expand in depth and size. In this study, periglacial water bodies in polygonal patterned ground not exceeding 30 m in diameter are termed polygon ponds while thaw lakes are characterized by larger size, greater depth and variable morphology. Water bodies exceeding 1000 m in diameter are considered to be thermokarst lakes. Thaw lakes and thermokarst lakes are assumed to represent advanced degradation stages of polygon systems (Meyer 2003; Grosse et al. 2013).

In total, 27 periglacial water bodies were studied. Fifteen were located in the alas, nine on the Berelekh River floodplain and three on the western yedoma ridge (Table 1). On the eastern yedoma ridge, ponds were absent. Among the water bodies studied, 12 were classified as intrapolygon ponds and six were interpolygon ponds.

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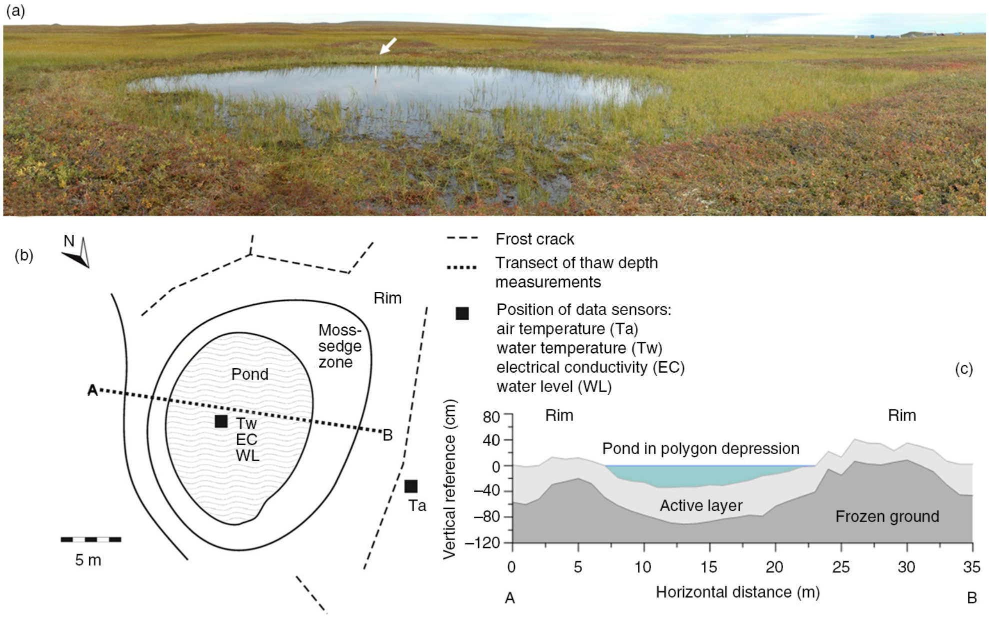

Fig. 3 Monitored site Kyt-01 covered an area of approximately 20 × 30 m; its central depression accommodated an 11.5 × 13.5 m wide intrapolygon pond. A boggy moss–sedge zone, polygon walls and frost cracks completely enclosed the pond. The polygon rims rose 0.3–0.4 m above the pond water table. The thaw depth below the pond centre was 40–58 cm while it was 19–24 cm at the polygon rims. (a) Photograph of monitored pond Kyt-01; an arrow indicates the position of the data sensors in the pond centre. View towards the east. Buildings in the background belong to the Kytalyk field station. (b) Schematic top view of the monitoring site with location of the data sensors. Active layer and ground surface elevation were measured along the A–B transect at 1-m resolution. (c) Schematic elevation profile along the A–B transect as measured on 26 August 2011. Zero on the vertical axis indicates the pond water level.

Three water bodies were grouped as thaw lakes (Supplementary Fig. S1, Kyt-19) and four water bodies were associated with rivulets (Supplementary Fig. S1, Kyt-13). The nine studied polygon ponds in the Berelekh River floodplain were characterized by water depths of 50 to >100 cm; the largest observed thaw depths were 45–50 cm. Intrapolygon ponds were typically shallow rounded water bodies located in the central depression of low-centre polygons (Supplementary Fig. S1, Kyt-04-16). The ponds were observed to have a slightly inclined bottom profile. In contrast, interpolygon ponds exhibited the most diverse morphology; for example, they could be X- or Y-shaped if they occupied troughs created by melting ice wedges (Supplementary Fig. S1, Kyt-14-18-22). These ponds were narrow but long and had steep, almost vertical or in some cases overhanging, peaty margins. Interpolygon ponds were 50–70 cm deep and contained little unfrozen organic substrate directly above the ice wedges. Thaw lakes were 70 to >100 cm deep and had steep margins (Supplementary Fig. S1, Kyt-19). Along their shorelines, polygonal microrelief indicated a flooded polygon landscape. Water bodies connected to a rivulet showed a vague polygonal structure (Supplementary Fig. S1, Kyt-13). Flowing water was not observed.

Table 1 Location, type, number and morphometry of the studied polygon water bodies according to major landscape unit and water type.

Landscape unit	*n*	Length (m)	Width (m)	Water depth (cm)	Thaw depth, pond (cm)	Thaw depth, rim (cm)
Alas	15	8–20	6–21	15–67	18–53	21–65
Yedoma	3	6–10	2–6	22–42	33–45	40
Berelekh River floodplain	9	10–50	5–50	50 to >100	20–45	45–50
Water body type	*n*	Length (m)	Width (m)	Water depth (cm)	Thaw depth, pond (cm)	Thaw depth, rim (cm)
Intrapolygon pond	12	5–25	7–21	15–70	35–53	21–65
Interpolygon pond	6	9–25	1–6	48–68	18–45	26–55
Thaw lake	3	50–100	10–20	70 to >100	no data	19–48
Other type	6	6–100	2–25	18 to >100	33 to > 100	32–48

Two oxbow lakes were studied in the Berelekh River floodplain. Both had a circular shape with diameters of 20–50 m and marginal thaw depths of around 50 cm.

Methods

This study combines spatial and temporal approaches. The ostracod record obtained is evaluated against physical properties such as substrate data, hydrochemical and meteorological data from different periglacial water bodies located in diverse landscape units at the point in time when each site was sampled. In addition, a monitoring set-up recorded continuous meteorological and limnological dynamics and the ostracod population at a selected pond site during the Arctic summer of 2011.

Field sampling and analyses

We caught >100 living ostracod individuals per site with a plankton net (mesh size 65 µm) and an exhaustor system, using the procedure explained by Viehberg (2002). The ostracods were subsequently stored in analytical alcohol (96%). Water was sampled 15 cm below the water table in all ponds in situ. Afterwards, pond substrate from the uppermost 5 cm at the substrate–water interface was collected. In addition, 22 rainwater and seven ground ice samples for water stable isotope ($\delta^{18}O$, δD) analyses were collected as references. Ground ice samples of different origin (ice-wedge ice, transient layer, ice lenses) were collected in drill holes and pits (Schirrmeister et al. 2012).

Hydrochemical parameters were analysed at the Kytalyk field station immediately after return from the field using titrimetric test kits (Viscolor: Acidity AC 7, Alkalinity AL 7, Oxygen SA 10, HE Total Hardness H 20 F). EC and pH were quantified by a WTW portable measuring device (pH/Cond 340i) equipped with a WTW TetraCon 925 conductivity cell for EC (reference temperature: 25°C) and a WTW Sentix 43-1 electrode for pH measurements. Samples for further hydrochemical and water stable isotope analyses were conserved in polyethylene bottles. Samples for ion composition analyses were filtered by a cellulose acetate filtration set (pore size 0.45 µm). Samples for cation analyses were treated with 200 µl nitric acid (65%).

Monitoring a polygon pond

A monitoring programme was carried out at a typical low-centred polygon pond (Kyt-01, Fig. 3). We visited the site at four-day intervals between 20 July and 26 August 2011 and collected sample packages, following a sampling protocol identical to that used at all other ponds in the study. In addition, the pond was instrumented with data sensors that measured specific values every 30 min (Supplementary Table S2) in order to assess temporal biotic and abiotic variability throughout the summer season. Water level data were computed with barometric compensation including air pressure and temperature data using HOBOware Pro software to convert raw pressure data to water levels and to compensate for barometric pressure changes. Air pressure data from the Kytalyk study site were kindly provided by J. van Huissteden (Faculty of Earth and Life Sciences, Vrije Universiteit Amsterdam). An active layer depth and ground surface elevation transect across the monitoring site was measured (Fig. 3). To obtain data about the surface microrelief and to establish a horizontal reference line, we used a so-called water level tube. A flexible tube with open ends was filled with water. Based on the position of the meniscus in the tube, we could construct a horizontal line, which was indicated using a string attached every 3 m to a wooden pole. We measured the ground surface elevation, the water table height and the active layer depth at 1-m intervals across the pond at the end of the field season (26 August 2011) when maximum thaw depths were expected.

Laboratory analyses of ostracods, substrate and water

Ostracod species identification was performed using a Zeiss Stemi SV II binocular microscope at ×12 magnification to determine valve characteristics and a Zeiss Axiolab binocular microscope at ×100 and ×400 magnification to determine soft-body characteristics. For taxonomic identification, ostracods were dissected and permanent slides of the soft body were prepared from three to five adult specimens of each sex and taxon, following Namiotko et al. (2011). Species characteristics were examined by using identification keys from Brehm (1911), Alm (1914, 1915), Bronštejn (1947), Pietrzeniuk (1977), Henderson (1990), Meisch (2000) and Fuhrmann (2012). Selected ostracod valves from all identified species were photographed at ×70 magnification with a Zeiss SMT GEMINI Ultra 55 Plus scanning electron microscope at the German Research Centre for Geosciences in Potsdam.

Pond substrate was analysed for grain size distribution using a LS 200 Beckman Coulter particle size analyser, mass specific magnetic susceptibility using a Bartington Instruments MS2 magnetic susceptibility meter (in $SI = 10^{-8}\ m^3\ kg^{-1}$) and the biogeochemical parameters TC, TOC, TN and TS using an Elementar Vario

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EL III elemental analyser. The biogeochemical values are given in weight percent (wt%). The TOC/TN ratio indicates the rate of mineralization of the organic substances and was calculated from the TIC value, which is the carbon remaining when TOC is subtracted from the TC content in%. All substrate samples were analysed for $\delta^{13}C$ using a Thermo Finnigan MAT Delta-S mass spectrometer. The values are expressed as delta per mil notation (δ, ‰) relative to the Vienna Pee Dee Belemnite standard with a reproducibility better than 0.15‰.

The ion composition of the pond water was assessed with inductively coupled plasma-optical emission spectrometry (Optima 3000 XL, Perkin Elmer) for elements interpreted as cations and ion chromatography (Dionex DX 320, Thermo Fisher Scientific) for anions. Pond, rainwater and ground ice samples were analysed for stable oxygen and hydrogen isotopes ($\delta^{18}O$, δD) using a Finnigan MAT Delta-S mass spectrometer (Meyer et al. 2000). The obtained values are expressed as δ, ‰ relative to the Vienna Standard Mean Ocean Water. The reproducibility of these data is ±0.8‰ for δD and ±0.1‰ for $\delta^{18}O$. In total, samples from 36 ponds, 22 precipitation events, three rivers and seven ground ice formations were measured.

Multivariate statistics

Non-metric multidimensional scaling was applied to the substrate (TOC, TN, TIC, grain size), hydrochemistry (EC, pH, alkalinity, acidity, water hardness, major ion content [values in%]) and ostracod data sets obtained from the ponds using the Vegan package, version 2.0-7 (Oksanen et al. 2013), with R software, version 2.15.1 (R Development Core Team 2008). The dimensions of the water bodies (length, width, depth) as well as water and air temperature information (all log-transformed) were included. Square-root transformation and Wisconsin double-standardization were applied and the Gower-Dissimilarity Index (substrate and hydrochemistry) or Bray-Curtis Dissimilarity Index (ostracods) was chosen. The ostracod record used for the non-metric multidimensional scaling analysis comprises the five most common taxa (Table 2): *Candona muelleri* ssp. *jakutica* Pietrzeniuk 1977, *Cyclocypris ovum* Jurine 1820, *Fabaeformiscandona krochini* Bronshtein (1947), *F. pedata* Alm 1947 and *Fabaeformiscandona* sp. Species that occur in a single sample of the record or in ponds with low ostracod abundances (Kyt-11; Table 2) as well as juvenile Candoninae were excluded from the analyses. For the monitored site Kyt-01, the ostracod species composition and the recorded environmental parameters from monitoring event no. six (9 August 2011), in the middle of the season, were chosen.

Results

Ostracod record in the Indigirka Lowland

A total of 4849 ostracod individuals were obtained from the 27 studied water bodies. Among the eleven observed ostracod taxa, eight were identified down to species level and two to the genus level, while one taxon comprises indeterminate juvenile Candoninae (Figs. 4, 5, Table 2). Species assemblages in the studied waters were clearly dominated by adult *Fabaeformiscandona pedata* (found in 25 ponds, 2381 individuals, 49%) and juvenile Candoninae (found in 26 ponds, 841 individuals, 22%). *Fabaeformiscandona pedata* is a typical representative of Arctic freshwater ostracods (Bronštejn 1947; Wetterich, Schirrmeister et al. 2008). *Candona muelleri jakutica* (found in 14 ponds), *F. krochini* (found in 12 ponds) and *Fabaeformiscandona* sp. (found in 12 ponds) were other common species. *Candona muelleri jakutica* is known from central and northern Yakutia (Pietrzeniuk 1977; Wetterich, Herzschuh et al. 2008) and the Lena River Delta (Wetterich, Schirrmeister et al. 2008). In contrast, *Cyclocypris ovum* occurred in 13 of 27 water bodies but with a low abundance of only one to five individuals per sample. *Cyclocypris ovum* inhabits shallow littoral zones of aquatic habitats with circumarctic distribution (Bronštejn 1947; Meisch 2000). Low numbers of *Cypria exsculpta* Fischer 1855, *Fabaeformiscandona harmsworthi* Scott 1899, *F. protzi* Hartwig 1898 and *F. groenlandica* Brehm 1911 were found in one pond each. A single empty valve from a cypridid ostracod (likely *Eucypris* sp.) was found in Kyt-26. *Cypria exsculpta*, *F. harmsworthi* and *F. groenlandica* were found as female specimens only.

Fabaeformiscandona harmsworthi is commonly distributed in east Siberia (Semenova 2003) and is known from ponds in the Lena River Delta (Wetterich, Schirrmeister et al. 2008). *Fabaeformiscandona protzi* is known to live in cold waters of mid-latitude regions in Europe and Russia (Bronštejn 1947; Meisch 2000) and was also found in periglacial water bodies of the Lena River Delta (Wetterich, Schirrmeister et al. 2008). *Fabaeformiscandona groenlandica* was first described by Brehm (1911) from findings on Greenland, on the Yamal Peninsula (north-west Siberia) and in the Novaya Zemlya Archipelago in the Arctic Ocean (Alm 1914). This first finding of *F. groenlandica* in the Indigirka Lowland in north-east Siberia extends its known distribution area eastwards to continental Siberia (Semenova & Sharapova 2012). *Fabaeformiscandona krochini* is another species that was

Table 2 Species list and counts of individuals per sample of freshwater ostracods from the Indigirka Lowland, north-east Siberia.

Site	*Candona müllerijakutica*	*Cyclocypris ovum*	*Cypria exsculpta*	*F.*[a] *groenlandica*	*F. harmsworthi*	*F. krochini*	*F. pedata*	*F. protzi*	*F.* sp.	*Eucypris* sp.	Juvenile Candoninae	Total
Kyt-01-01							2				81	83
Kyt-01-02							8				64	72
Kyt-01-03							19				60	79
Kyt-01-04							22				96	118
Kyt-01-05		1					20				62	83
Kyt-01-06		1					65				39	105
Kyt-01-07							62				60	122
Kyt-01-08	1						44		1		34	80
Kyt-01-09							74				30	104
Kyt-01-10							112				32	144
Total Kyt-01	1	2					428		1		558	990
Kyt-02		1				1	62				107	171
Kyt-03	11					15	21				44	91
Kyt-04		1				7	62				52	122
Kyt-05		1				4	120				30	155
Kyt-06						2	25				37	64
Kyt-07	5						33		6		29	73
Kyt-08	29	1					56		28		1	115
Kyt-09	6	2					12		5		31	56
Kyt-10	68	3		8			372		133		163	747
Kyt-11	3										1	4
Kyt-12						1	54				32	87
Kyt-13	4					1	120				5	130
Kyt-14							382				13	395
Kyt-15	1	1					18		4		2	26
Kyt-16	6						134		6		15	161
Kyt-17					2	1	123				19	145
Kyt-18	16						61		16		1	94
Kyt-19						9	126				87	222
Kyt-20	5	1					122		38		6	172
Kyt-21			1				139		2		0	142
Kyt-22	3	1					22		3		1	30
Kyt-23	7	1					56		12		88	164
Kyt-24		5				5	99				14	123
Kyt-25						28	57				15	100
Kyt-26		1				6	105	27	4	1	36	180
Kyt-27	40								38		12	90
Total Kyt-2-27	204	19	1	8	2	80	2381	27	295	1	841	3859
Total all	205	21	1	8	2	80	2809	27	296	1	1399	4849

[a] *Fabaeformiscandona*.

newly found in the study area. *Fabaeformiscandona* sp. could not be entirely identified with the present taxonomic literature. Males are larger (1.3 mm) than females (1 mm). The female's valve is characterized by a straight ventral margin and slight concave bulges at the anterior and posterior dorsal valve (Fig. 4, nos. 9, 10). The valve of male *Fabaeformiscandona* sp. has a pronounced bulge in the ventral margin and a bend in the dorsal margin of the valve (Fig. 4, nos. 11, 12). The valve morphology is similar to *F. fabaeformis*, but the soft-body morphology is not entirely consistent with that species. However, the identification to the genus level based on soft-body characteristics, such as the morphology of the cleaning limb, mandibular palps with smooth γ-setae, the second segment of the mandibular palp and the uropod, clearly points to *Fabaeformiscandona*. The copulation organ of female *Fabaeformiscandona* sp. is similar to female *F. pedata*. The Zenker organ of male *Fabaeformiscandona* sp. has seven rings of spines. *Fabaeformiscandona* sp. can tolerate the smallest range in EC and the lowest concentrations of major ions in the pond waters (Supplementary Fig. S4).

Figure 5 presents the ostracod record with respect to the location of the water bodies in the major landscape units. Six out of 12 taxa (*C. muelleri jakutica, Fabaeformiscandona* sp., *C. ovum, F. krochini, F. pedata*, juvenile Candoninae) were present in ponds located in all landscape units. The species diversity in a single

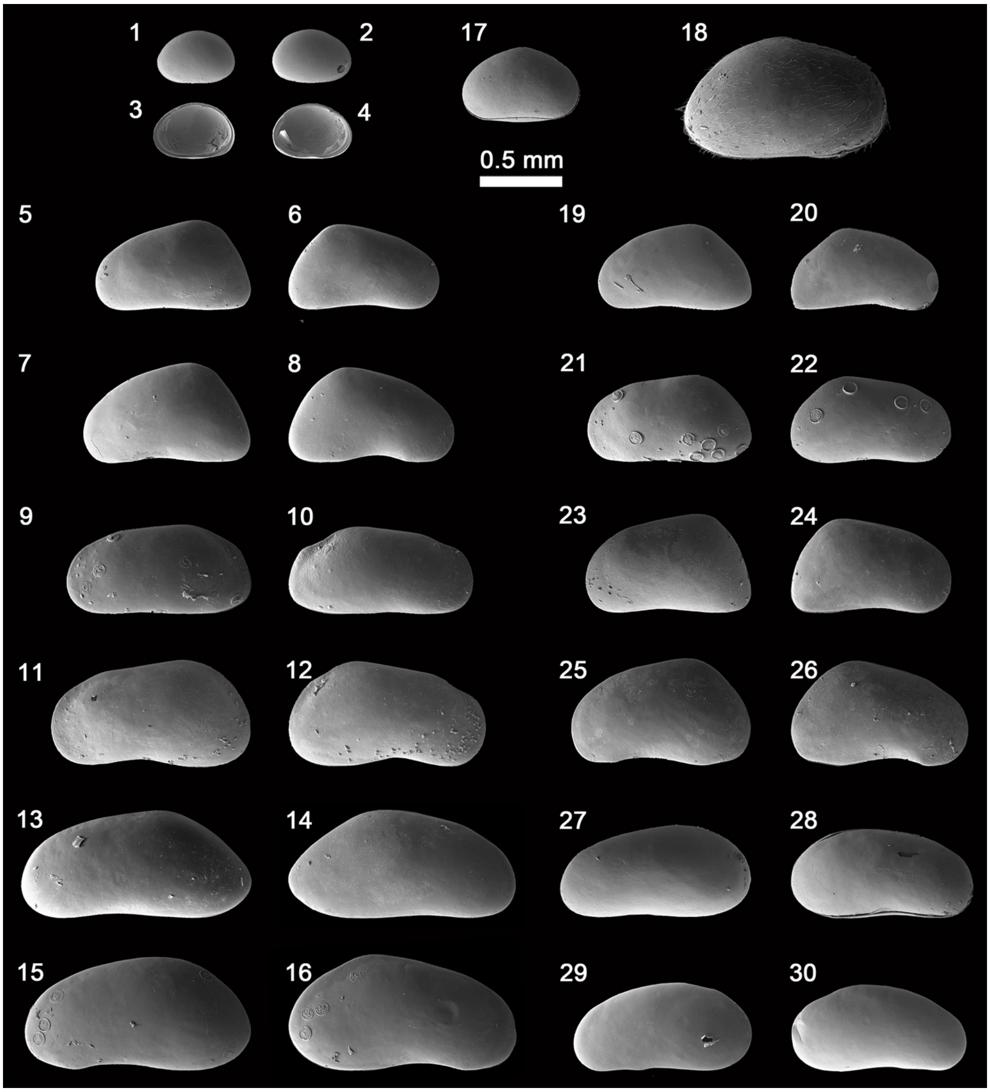

Fig. 4 Scanning electron microscope images of ostracod valves from the Indigirka Lowland. *Cyclocypris ovum*: (1) female left valve (LV), (2) female right valve (RV), (3) female RV inner view, (4) female LV inner view; *Fabaeformiscandona krochini*: (5) female LV, (6) female RV, (7) male LV, (8) male RV; *Fabaeformiscandona* sp.: (9) female LV, (10) female RV, (11) male LV, (12) male RV; *F. pedata*: (13) female LV, (14) female RV, (15) male LV, (16) male RV; *Cypria exsculpta*: (17) carapace; *Eucypris* sp.: (18) RV; *Fabaeformiscandona harmsworthi*: (19) female LV, (20) female RV; *F. groenlandica*: (21) female LV, (22) female RV; *Candona muelleri jakutica*: (23) female LV, (24) female RV, (25) male LV, (26) male RV; *F. protzi*: (27) female carapace, left side, (28) female carapace, right side, (29) male LV, (30) male RV.

pond comprised two to seven taxa including juvenile Candoninae. Water bodies located in the Berelekh River floodplain hosted the highest observed ostracod diversity per pond (three to seven taxa). In addition, three taxa appeared in floodplain waters exclusively: *C. exsculpta* (Kyt-21), *F. protzi* and *Eucypris* sp. Ponds in the alas and on the yedoma hosted up to seven taxa. The ostracod assemblage in the three ponds on the western yedoma ridge was characterized by abundant *C. muelleri jakutica* and *Fabaeformiscandona* sp. *Fabaeformiscandona groenlandica* was found in one pond (Kyt-10) on the yedoma ridge only.

The ostracod record with respect to different water types showed that the highest number of taxa in total (10 taxa) and per pond (three to seven taxa) occurred in intrapolygon ponds. Beside *F. pedata* and juvenile Candoninae, *F. krochini* was relatively common and reached its largest abundance in intrapolygon ponds. Intrapolygon ponds hosted the highest ostracod species diversity (10 in total, three to seven per pond), while the ostracod diversity was lower in the other pond types and lowest in thaw lakes. The ostracod species diversity in polygon ponds in the Indigirka Lowland was comparable to that

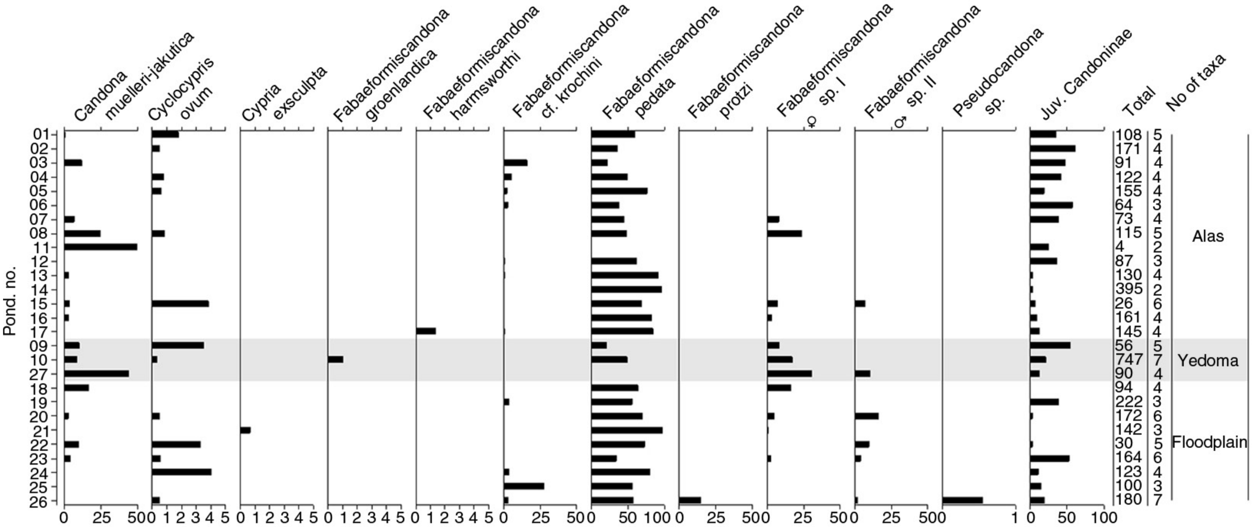

Fig. 5 Ostracod record (number of complete carapaces) from 27 studied water bodies in the Kytalyk area in percent, grouped according to the major landscape units. Note varying scales.

found in similar studies. For example, thermokarst lakes in central Yakutia hosted 15 species, while nine were present in periglacial water bodies in north-east Yakutia and 14 in water bodies in the Lena River Delta (Wetterich, Schirrmeister et al. 2008). Seven ostracod species were found in 24 ponds in Arctic Canada (Bunbury & Gajewski 2009). The pattern of dominance by a few species seems to be common for Arctic ostracod assemblages.

The outcomes of a multivariate statistical analysis combining the pond's substrate and hydrochemical properties as well as the ostracod assemblages are presented in Fig. 6. Stress values of 14.14% (substrate properties), 14.21% (hydrochemistry) and 13.45% (ostracods) indicated a low geometrical deformation. The statistical evaluation highlighting substrate properties (Fig. 6a) reveals that organic content (TOC and TN) was highest in deep lakes located in the alas while TIC content was highest in lakes with increased water hardness located in the Berelekh River floodplain. The non-metric multidimensional scaling analysis highlighting hydrochemical parameters (Fig. 6b) suggests a zonation between typically large water bodies with high alkalinity that are often located in the floodplain and water bodies with an increased amount of Na, K and Cl which are common in the alas. The assessment focusing on ostracod assemblages (Fig. 6c) reveals that *F. pedata* and *F. krochini* are common in large, shallow polygons that are also characterized by high alkalinity. *Candona muelleri jakutica* and *Fabaeformiscandona* sp. occur preferentially in smaller ponds that are located on the yedoma, while *C. ovum* is common in shallower, smaller ponds.

Population dynamics of *F. pedata*

The population record of *F. pedata* at the monitored site Kyt-01 yields detailed insights into this organism's life cycle with regard to the juvenile/adult and male/female ratios throughout the 2011 summer (Fig. 7). During 40 days, in total 990 ostracods were caught in pond Kyt-01. The dominating taxa of the Kyt-01 ostracod population were adult *F. pedata* and juvenile Candoninae. It is most likely that the unidentified juvenile Candoninae mainly comprise instars of *F. pedata*. In addition, two individuals of *C. ovum*, one individual of *C. muelleri jakutica* and one individual of *Fabaeformiscandona* sp. were found. The population structure of *F. pedata* in Kyt-01 during the summer of 2011 shows that the proportion of juvenile *F. pedata* declined from about 98% to 22% when they were growing to adulthood. Adult male specimens were present early and their proportion remained stable at a low level, between 11 and 18%. In contrast, adult female specimens appeared from early August and reached high numbers. At the end of the 2011 summer, 66% of the entire *F. pedata* population in Kyt-01 were mature female specimens. Thus, the ostracod assemblage in the monitored pond was not only dominated by *F. pedata* but also by adult female specimens from early August on.

Logistic constraints prevented us from monitoring the pond's ostracod population from the moment when it became ice-free. Given the extremely low winter temperatures and shallow depth of the pond, it is unlikely that individuals from the previous season would have survived the winter since the ponds and the substrate freeze solid. We therefore assume the new population

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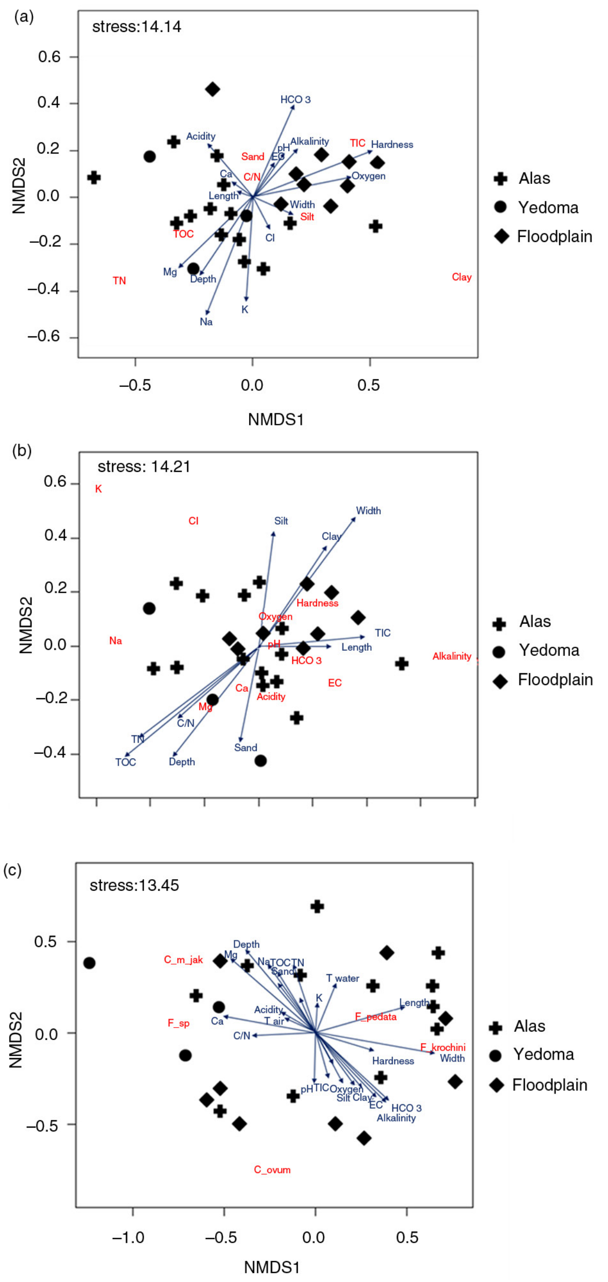

Fig. 6 Non-metric multidimensional scaling biplot of the (a) substrate properties, (b) hydrochemical variables and (c) ostracod species assemblages according to the major landscape units. Environmental parameters are superimposed. Species names are abbreviated as follows: *Candona muelleri jakutica* (C_m_jak), *Cyclocypris ovum* (C_ovum), *Fabaeformiscandona pedata* (F_pedata), *F. krochini* (F_krochini) and *Fabaeformiscandona* sp. (F_sp).

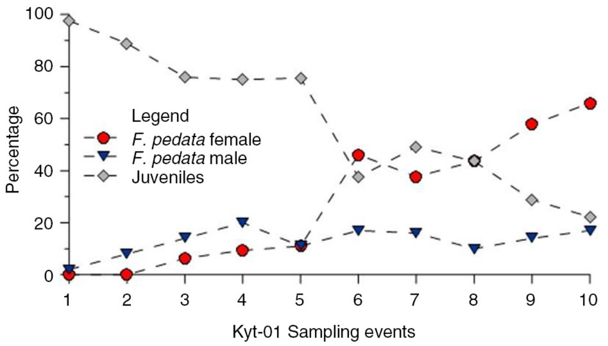

Fig. 7 Population structure of *Fabaeformiscandona pedata* in the monitored pond Kyt-01 throughout the summer season from 20 July 2011 to 25 August 2011, measured at four-day intervals.

arises entirely from freezing-resistant eggs from the previous year. The high percentage of juveniles at the beginning of the summer season (Fig. 7, Table 2) and the early but low presence of adult males point towards the males being the first individuals of the new population to hatch, moult and mature. Male individuals of *F. pedata* probably have an earlier and faster development cycle than females.

The intermediate increase of juveniles in mid-August is time-lagged to the increase of female adult *F. pedata* (Fig. 7) and points to newly produced juvenile specimens of the present year. Repeated sampling in early July 2012 in the monitored pond revealed the presence of abundant juvenile Candoninae, up to 10 female and nine male specimens of adult *F. pedata* and up to 10 specimens of *C. muelleri jakutica*.

Substrate properties in polygon ponds

The biogeochemical substrate properties offered largely homogeneous habitat conditions to ostracods. The pond substrate consisted of unconsolidated fine-grained, organic-rich material (Supplementary Fig. S2). The material was characterized by a multimodal grain size distribution with 10–20% clay, 30–70% silt and up to 30% fine-grained sand and 10–20% medium- and coarse-grained sand. The magnetic susceptibility ranged from 28 to 50 SI, with a stronger variance up to 66 SI at sites located in the Berelekh River floodplain. Occasionally, plant fragments, roots, rhizomes and leaves were observed in different decomposition stages. TIC content in the pond substrate was on average 1.6 wt%. The TOC content was around 30 wt%. At sites located in the river floodplain, the lowest amounts of TOC (11 to 26 wt%) were found while substrate from ponds in other landscape units contained considerably higher TOC (26–50 wt%). TN content of the pond substrate was on average 2–3.5 wt%, but it was lower in ponds located on the river floodplain (1 wt%). The substrate was characterized by TOC/TN ratios ranging from 11 to 20. The δ^{13}C value in the substrate averaged $-32‰$. The maximum values of TOC/TN (20) and δ^{13}C ($-30‰$) were reached in pond Kyt-27, located on the yedoma ridge. TS content of the substrate was low at 0.2 wt%. Site Kyt-06 had the highest S content of 0.4 wt%. Biogeochemical substrate properties with regard to water types revealed that TOC in interpolygon ponds was <25 wt% while substrate from intrapolygon ponds contained from 33 to 44 wt% TOC. A similar differentiation between those two water types existed for TN amounts in pond substrate. Intrapolygon ponds were observed to contain around 3 wt% of TN and a TOC/TN ratio of 12.5, while interpolygon ponds contained around 1 wt% of TN and a higher TOC/TN ratio of 14.7.

Pond water hydrochemistry and water stable isotopes

Measurements of pH indicated that the ponds were acidic to circumneutral, ranging from 5.5 to 7.1 in water bodies from all studied landscape units and water types. The water hardness varied from 1.5 to 7.5°dH. Polygon ponds displayed little variability of acidity (0.4 mmol l^{-1}) and alkalinity (0.2–1.6 mmol l^{-1}). The amount of dissolved oxygen in the studied water bodies ranged between 5.4 and 11.8 mg l^{-1}. Furthermore, the EC was low at 19–53 µS cm^{-1}. The major ion composition of the studied water bodies was characterized by similar amounts of dissolved cations and anions (Supplementary Fig. S3). The water bodies contained on average 3.6 mg l^{-1} calcium (Ca), 2.0 mg l^{-1} magnesium (Mg), 0.9 mg l^{-1} sodium (Na) and 0.6 mg l^{-1} potassium (K). All water bodies contained about 11.5 mg l^{-1} hydrogen carbonate (HCO_3) and 0.4 mg l^{-1} chlorine (Cl), while sulphate (SO_4) components were below the detection limit. The relative concentration of cations in the ponds was Ca > Mg > Na > K, while the relative concentration of anions was $HCO_3 > Cl$. The dissolved ion content was congruent with the water from the two sampled rivers (Konsor Syane, Berelekh), but 1.5 mg l^{-1} SO_4 was present in the Berelekh River. The river water EC was 21 to 22 µS cm^{-1} and the pH ranged between 6.3 and 6.4. The pond water was clear, or brownish or reddish in colour.

Hydrochemical data from 10 monitoring events in Kyt-01 revealed that the mean value was about pH 6.3 (Fig. 8), and alkalinity and acidity values of 0.4 mmol l^{-1} were rather stable throughout the monitored time period. In contrast, the dissolved oxygen content of the pond water varied between 6.0 and 10.8 mg l^{-1}. The ionic composition of the monitored pond was similar to the other 26 studied water bodies, but here we observed some variability over the summer season: The amount of dissolved Ca doubled from 1 to 2 mg l^{-1} while the concentration of dissolved Na and K declined by half, from around 1.0–0.5 mg l^{-1}. HCO_3 ranged between 2.4 and 6.7 mg l^{-1}. The relative concentration of cations changed from Ca > Na > Mg > K to Ca > Mg > Na > K after precipitation events, but the relative concentration of anions was constantly $HCO_3 > Cl$. The amount of dissolved oxygen as well as the HCO_3 content increased towards the end of the season when air and water temperatures decreased.

Figure 9 summarizes the water stable isotope composition of pond and rainwater in summer 2011 compared to the Global Meteoric Water Line, which represents the average isotopic relationship in global precipitation (Craig 1961). The isotopic composition of rainwater ($n = 22$) ranged between −21.7 and −11.8‰ for $\delta^{18}O$ and from −163 to −101‰ for δD while $\delta^{18}O$ values from ponds ($n = 36$) varied between −19.0 and −12.9‰ and pond δD was between −146 and −117. Based on the systematic deviation of local rainwater towards values below the Global Meteoric Water Line, a function representing the 2011 summer precipitation (slope of 6.53, $R^2 = 0.93$) was deduced. Compared to local precipitation and the global mean, the deviation in pond waters was most pronounced and is expressed in a local evaporation line (slope of 4.91, $R^2 = 0.93$).

In contrast to the data set from the 26 ponds assembled from one-time measurements, the monitored pond was sampled at four-day intervals over a time period of six weeks. Aligned $\delta^{18}O$ values from intrapolygon ponds of between −15 and −12‰ (Fig. 9) were documented at the monitored site Kyt-01. The stable isotope composition of Kyt-01 water therefore appears to reflect variations throughout the 2011 summer season. Ponds located in the river floodplain were characterized by water stable isotope values that corresponded closely to the isotopic composition of the Berelekh River water. Obviously, the ponds are flooded by the river in spring. While the stable river water isotope composition was very similar to that of the pond water and rainwater, ground ice sample values were scattered across a broad range. Data points clustering around −25‰ for $\delta^{18}O$ and −200‰ for δD were derived from an ice wedge. The remaining data points represent samples taken from the transient layer and ice lenses. The overall similar water stable isotope composition in local rain and pond water suggests rainwater as the primary water source for the ponds that underwent evaporation. River flooding and meltwater from ground ice are considered as secondary water sources.

Meteorological monitoring

The records of all sensors (Supplementary Table S3) installed at the monitored pond Kyt-01 are presented in Fig. 8a–c. The recorded air and water temperatures

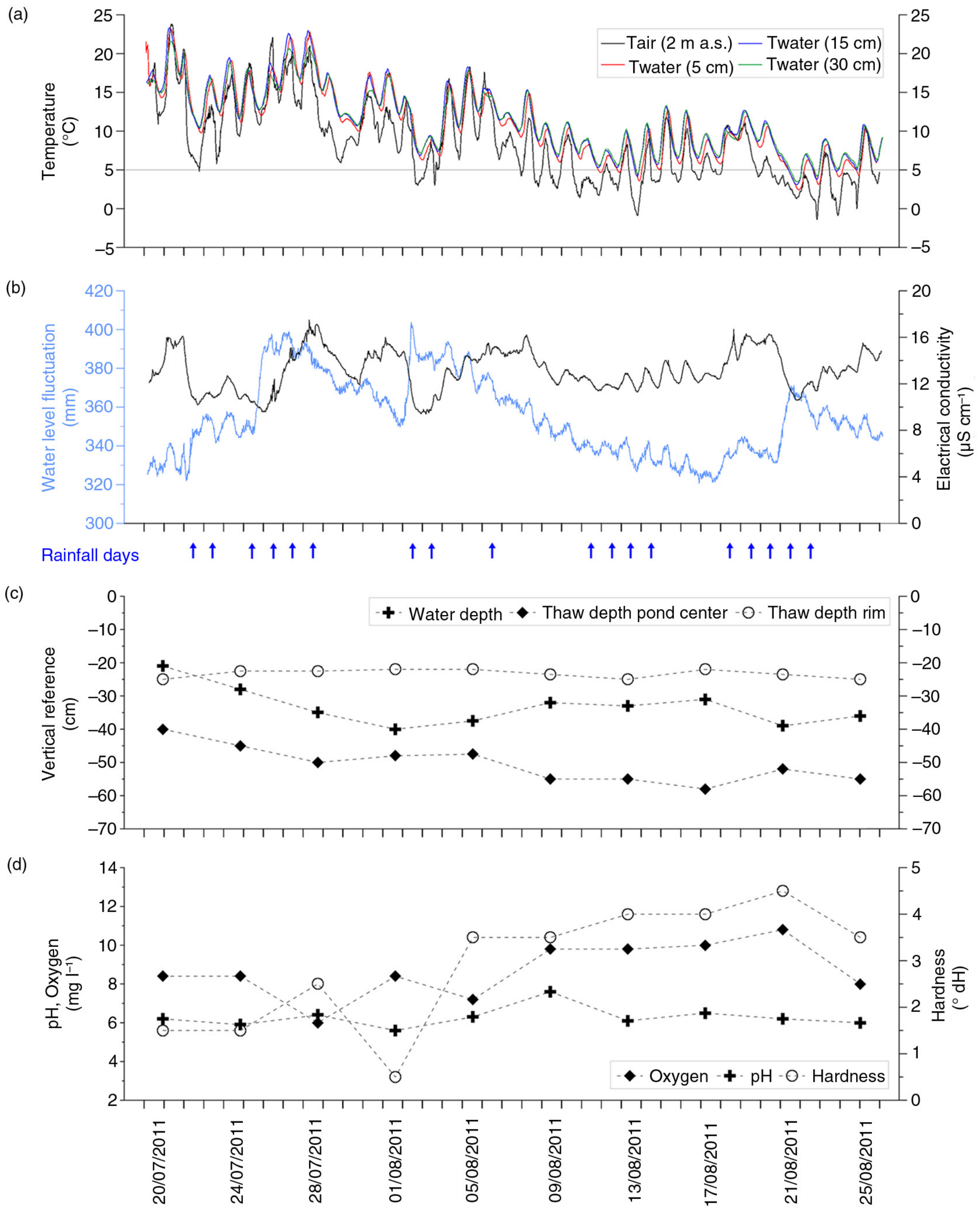

Fig. 8 Monitoring data obtained at the Kyt-01 site from 29 July to 16 August 2011. (a) Air and water temperatures at different depths. (b) Electrical conductivity and water level; rainfall days are marked according to our rainwater sampling for stable isotope analyses and rain gauge measurements (pers. comm. J. van Huissteden, Vrije Universiteit Amsterdam, Faculty of Earth and Life Sciences, The Netherlands). (c) Thaw and water depth in the pond, and thaw depth in the adjacent polygon rim as measured by hand. (d) Selected hydrochemical properties of the monitored pond Kyt-01 obtained during the 10 monitoring events in summer 2011. Note varying scales.

(Fig. 8a) fluctuated daily by about 10°C and a cooling trend was superimposed on these records towards the end of the monitored time period in autumn 2011. The recorded mean air temperature over the six-week period was 8.5°C with a maximum of 23.8°C and a minimum of −1.4°C. The water temperature ranged from 10.9 to 11.4°C, with a maximum of 21.6 to 23.3°C and a minimum of 2.4 to 3.4°C at different water depths. Overall temperature fluctuations during the summer season exceeded 20°C in the uppermost 15 cm of the water

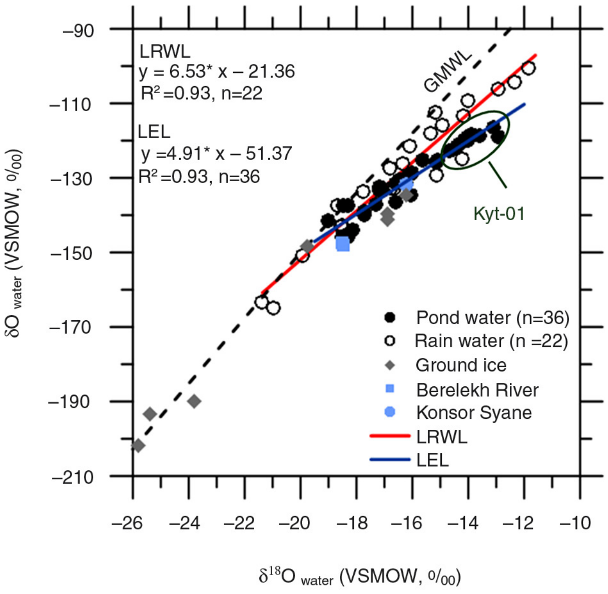

Fig. 9 Stable isotope record of δD and δ^{18}O from rain and all sampled ponds, ground ice and river water in the Kytalyk study area in summer 2011 relative to the Vienna Standard Mean Ocean Water (VSMOV). Global Meteoric Water Line (GMWL) after Craig (1961). Local evaporation line is abbreviated as LEL and local rain water line as LRWL.

column (5 cm: 20.8°C; 15 cm: 20.2°C) and were still high at 18.2°C near the pond bottom at 30 cm depth. Air and water temperatures showed similar patterns (Fig. 8c), indicating that the temperature of shallow water bodies seems to be closely tied to the prevailing air temperature. Thermal stratification in the pond was absent.

During summer 2011, the mean water depth was 35 cm but water level fluctuations of ±8 cm occurred (Fig. 8c). The maximum water depth measured was 40 cm at the end of July; the pond had grown shallower (32 cm) in mid-August. The water level displayed diurnal variations of about 10 mm that were triggered by air-temperature-induced evaporation and precipitation events. For example, during rather warm days (26–28 July; 31 July–1 August; 4–6 August) the water level declined by 2–3 cm. In contrast, rainfall on 25 July and 2 and 21 August resulted in an abrupt water level increase of 4–5 cm (Fig. 8b).

Variations in pond water temperature and EC accompanied temperature fluctuations throughout the water column (Fig. 8b). Measured values of EC ranged from 9.2 to 15.1 µS cm^{-1} with a mean of 12.0 µS cm^{-1}. The EC followed patterns in air temperature variation; warmer weather conditions (21–22/07, 26–29/07, 31/07–01/08, 04–08/08, 18–20/08; 10–20°C) resulted in higher EC ($>$16 µS cm^{-1}), while colder weather (22/07, 30/07, 03/08; 21/08; $<$5°C) was accompanied by lower conductivity values ($<$12 µS cm^{-1}) due to enhanced or reduced evaporation, respectively. Distinct diurnal fluctuations in pond water level and EC between 13 and 16 August 2011 demonstrated the close linkage between air and water temperature, water level and EC in shallow polygon ponds.

The water depth as measured by hand in the pond centre corresponded to the data derived from the sensor (Fig. 8c). The thaw depth of 24 cm in the polygon rim was rather stable, while the thaw depth in the pond centre was twice as deep and increased by about 20 cm from 40 cm in July to 58 cm in mid-August.

Discussion

Polygon waters as habitat for freshwater ostracods

In the pond substrate, the δ^{13}C values reflect an organic carbon source from terrestrial plants conducting C3-photosynthesis (Layman et al. 2012). The substrate was characterized by TOC/TN ratios which are typical for sediments with a high degree of decomposition (Hansen 1961) in waterlogged environments in high-latitude regions. Sulphur compounds in the pond water and substrate are subject to microbial breakdown by sulphate-reducing bacteria (Rabus et al. 2006; Wagner 2008). The substrate composition is typical of cryosols incorporated in late Pleistocene Ice Complex deposits occurring in the study area around Kytalyk (Lavrušin 1963; Kaplina et al. 1980) and generally in the north-eastern Siberian coastal lowlands (Schirrmeister et al. 2013; Strauss et al. 2013).

Polygon ponds in the Indigirka Lowland were typically well-oxygenated, dilute and oligotrophic, with slightly acidic to circumneutral pH. Dissolved oxygen was present throughout the entire water column due to wind-induced mixing of these shallow water bodies. Oxygen may also enter the water column via rainfall or originate from primary production in water and wetland plants. Well-oxygenated conditions in polygon ponds are also indicated by benthic organisms such as ostracods. The circumneutral pH value points to precipitation as the major water source. Rainwater has a pH of 7 in the Kolyma Lowland (Schirrmeister, unpubl. data) and a pH between 4 and 7 in northern Canada (Schindler et al. 1976; Welch & Legault 1986) but shows high seasonal and interannual variability. Beermann & Kokhanova (2012) found pH values between 4 and 6.4 in soil water from the Kytalyk study area. Here, microbial degradation of organic matter releases humic substances that enter the ponds via percolating rainwater and decrease their pH. Therefore, the brownish to reddish water colour is attributed to the presence of dissolved organic matter (Rautio & Vincent 2006; Rautio et al. 2011). The low EC in pond water also indicates that precipitation is an important water supply.

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Flooding adds river water with low EC to ponds located in the floodplain and further dilutes them. In contrast, thawing releases ions that were previously trapped in the frozen ground, which may then enter the pond water and increase the EC: the ion content of ice-wedge ice on the Oyogos Yar coast at the northernmost Indigirka Lowlands ranged from 40 to 58 µS cm^{-1} at a pH value of 6 to 6.5 (Opel et al. 2011).

Based on weather and water level observations (Fig. 8) and similarities in water stable isotope signatures between precipitation and pond water (Fig. 9), rainfall is identified as the major water source for polygon ponds. The low ion content of precipitation (Welch & Legault 1986) explains the dilute character of periglacial water bodies and highlights the role of summer precipitation in filling polygon ponds and other small periglacial freshwater bodies. Additionally, meltwater from snow contributes to the initial composition of periglacial water bodies in spring (Prowse et al. 2006). The hydrochemical and isotopic fingerprints of these water bodies indicate that meltwater from ground ice and, especially, river water, during spring floods are additional sources.

We used physical and chemical baseline data from the ponds to characterize habitat and to determine ecological tolerance ranges in the freshwater ostracod species that were present (Supplementary Table S4). The five most common taxa of the ostracod record from the Kytalyk study area (*Candona muelleri jakutica, Cyclocypris ovum, Fabaeformiscandona pedata*, *F. krochini, Fabaeformiscandona* sp.) were evaluated against 12 selected environmental parameters (pH value, dissolved oxygen content, water temperature, water depth, hardness, EC and all major ions). All tested taxa reacted most clearly on water hardness, EC and the major ions dissolved in the pond water. Variations in pH value, dissolved oxygen content, water temperature and water depth caused less pronounced responses. *Fabaeformiscandona pedata* and *F. krochini* displayed the widest range of all environmental parameters while *Fabaeformiscandona* sp. accepted the lowest ranges of EC and the tested dissolved ions. However, those data represent the ranges of environmental parameters of the tested species in the Kytalyk study area. In order to explore the complete ecological range of a certain species, all available findings and environmental records need to be considered.

Landscape scale spatial variability

Biogeochemical and physical properties of the pond substrate as well as the overlying water column vary within narrow ranges. Polygon water bodies in the Indigirka Lowland therefore offer largely homogeneous habitat conditions to benthic ostracods. However, the sedimentological, hydrochemical and water stable isotope composition of water bodies located in the Berelekh River floodplain differ from those of water bodies located in other landscape units. Floodplain ponds were characterized by considerably lower TOC and TN content as well as lower EC while magnetic susceptibility was increased. Those variations are attributed to river flooding in spring. Clastic sediment material transported by the Berelekh River is dispersed across the floodplain; it lowers the TOC, TN and concentration of ions in the pond water, and increases the amount of magnetic mineral particles in the pond substrate. In addition, the similarity in water stable isotope composition of river water and floodplain ponds indicates that ponds located in the close vicinity of the current river course are flooded in spring. The more depleted isotopic signal of the river water itself and river-water-influenced ponds results from source water of mixed isotopic composition. River water sources differ in type, age and origin: rainwater, meltwater from snow and different types of melting ground ice drain over land into the river. With respect to air temperatures and large-scale patterns in atmospheric circulation, the stable isotope composition in snow is more negative than in rain (Welch & Legault 1986). According to Meyer et al. (2002) and Opel et al. (2011), ice wedges of Holocene age in the Laptev Sea region have a δ^{18}O value of -26 to -21‰ while ground ice of late Pleistocene age in the same area is characterized by more depleted δ^{18}O values of about -30‰. In ice wedges that were sampled during the 2011 field campaign, δ^{18}O values of -16‰ to -25‰ were found which represent most likely Holocene-to-modern-aged ice wedges (unpubl. data). The stable oxygen isotope signature of modern local summer precipitation is -16‰. Water input from melting late Pleistocene ground ice may therefore shift the water stable isotope composition of river water towards more negative values. Since the studied ponds accommodate small water volumes owing to their shallowness and small size, flooding events have a considerable influence on substrate geochemistry, pond water hydrochemistry and water stable isotope composition.

Among the different water body types, intrapolygon and interpolygon ponds differ in morphology as well as biogeochemical properties. Intrapolygon ponds are characterized by larger but shallower open water areas compared to the long and narrow shape of deep interpolygon ponds. In intrapolygon ponds, a larger surface: depth ratio allows for quick warming and good mixing of the water column. Furthermore, a relatively thick layer of thawed substrate isolates the pond bottom from the cold underlying permafrost. Intrapolygon ponds are commonly colonized by extensive wetland flora (mainly Cyperaceae) along the shores whose organic material enters the ponds at the end of the vegetation period every autumn. In contrast, interpolygon ponds are deep and narrow with a thin layer of thawed substrate above the melting ice wedge. Interpolygon ponds usually have steep margins and reach depths which do not allow extensive wetland flora to grow. TOC and TN content were higher in intrapolygon ponds than in interpolygon ponds. The morphology of the water body controls the organic content through the presence or absence of wetland flora.

In general, the non-metric multidimensional scaling (Fig. 6c) reflects a rather homogeneous ostracod species distribution; species that occur preferentially in certain pond types or certain landscape units are lacking. Since ostracods do not actively migrate on landscape scale, but spread passively across large distances, their distribution is related to the largely homogeneous habitat conditions and rather close vicinity of the sampling sites. Both eggs and living ostracods can travel in the feathers or gut of aquatic birds, in the fur of mammals and by wind, and thus spread over larger areas (Meisch 2000; Brochet et al. 2010; Smith & Delorme 2010). In the Kytalyk study area, Siberian snow cranes (*Leucogeranus leucogeranus*) and other birds as well as Arctic foxes (*Vulpes lagopus*), reindeer (*Rangifer tarandus*) and moose (*Alces alces*) are common animals in the tundra and may allow the ostracods to migrate between ponds.

Temporal variability in polygon ponds

At the monitored pond, Kyt-01 temporal fluctuations in water temperature and hydrochemical and physical properties were recorded along with a detailed population record of the dominant species *F. pedata*. The short ice-free period in the Arctic summer sharply limits the time frame available for ostracods to traverse all instar stages, and does not allow all juvenile ostracods to mature. However, field studies and laboratory experiments of *Tonnacypris glacialis* showed clearly that only one generation of this ostracod species occurs during the growing season on Svalbard (Wojtasik 2008), and that the eggs of that particular species require freezing temperatures to allow the next generation in the following year to hatch.

The juvenile/adult and male/female ratios in an Arctic ostracod population are determined by the timing of thawing and freezing of their habitats, but also the species-specific life cycle.

Parthenogenesis is common among northern ostracod populations and in Arctic species (Little & Herbert 1997; Meisch 2000). Parthenogenetic ostracods were found to cover a wide geographic range and to have a high potential for dispersal, and they are able to withstand short-term variations in habitat stability (Martens et al. 2008). However, their genetic diversity is reduced and rare males, such as found for *F. pedata* in Kyt-01, would be functionless in a pure parthenogenetic population. The small number of males, which can fertilize several female specimens, therefore suggests that sexual reproduction of *F. pedata* occurs. The sexual mode of reproduction allows them to survive in temporary habitats such as polygon ponds by maintaining high genetic diversity, and also enabling a rapid reproductive cycle (Meisch 2000; Smith & Delorme 2010). The population dynamics of Arctic ostracod species hold out an as-yet unexplored potential to identify changes in the climate-driven environmental conditions of their habitats.

In the pond water, an increase in dissolved oxygen content from 8 to 10 mg l^{-1} and in water hardness from 2 to 4°dH (Fig. 8d) is attributed to the higher dissolubility of gases and ions in colder water. The ion concentration changed during intense rainfall from 24 to 28 July. An increase in HCO_3 and water hardness is related to CO_2 entering the pond water via diffusion and rain drops. Moreover, the change in relative cation concentrations from $Ca > Na > Mg > K$ to $Ca > Mg > Na > K$ after rainfall highlights the impact of precipitation events on small water bodies with very low ionization. The monitored pond underwent strong diurnal and seasonal fluctuations in water temperature throughout the entire water column and closely tracked the ambient air temperature. Small and shallow water bodies immediately respond to variations in air temperature because wind-induced mixing and wave action creates identical water temperatures at all depths, as has also been observed by Wetterich, Schirrmeister et al. (2008) and Boike et al. (2013). Consequently, shallow periglacial water bodies are polymictic. Daily fluctuations in air and water temperature were superimposed by a general cooling trend towards autumn. Similar fluctuations in water and air temperature of shallow ponds and lakes were recorded over several years in polygon ponds on Alaska's North Slope (Hobbie 1980) and the Lena River Delta in Russia (Boike et al. 2008; Boike et al. 2013). Multi-year solar radiation measurements taken during the study of the Lena River Delta demonstrated that air and water temperatures follow variations in incoming radiation. Air temperature fluctuations were accompanied by variations in EC and water level which are caused by

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precipitation and temperature-induced evaporation that raises or lowers the ion concentration in the water during warmer or colder periods.

Water level changes are driven by evaporation and precipitation events. In addition to water added directly to the pond by rain, water from a polygon pond's catchment which reaches up to the crests of the polygon rims also flows into the central water body. The percolation of the water through the thawed layer in the catchment slightly delays the water level response. Wind- and air-temperature-driven evaporation subtracts water from the ponds. In addition, the ongoing thawing process below the water body targets formerly frozen pond substrate and releases an unknown amount of meltwater that was previously trapped in ground ice, which now becomes part of the pond. However, the effects of air-temperature-induced evaporation and summer precipitation predominantly drive the hydrochemical and hydrological regime in small and shallow ponds.

Long-term observations in Alaska, Siberia and Canada have revealed that changes in meteorological conditions and permafrost cause major shifts in the hydrological parameters of lakes and ponds. Subsurface drainage of permafrost ponds ($>$10 m diameter) through degradation of shallow permafrost ($<$30 m thickness) and the formation of taliks has decreased the surface area of tundra ponds on the Seward Peninsula, Alaska, over the past 50 years (Yoshikawa & Hinzman 2003). A similar decline in lake area and abundance has occurred in northern Siberia since 1973 owing to subsurface drainage through discontinuous permafrost (Smith et al. 2005). Labreque et al. (2009) observed a reduction in lake surface area at a study site in the northern Yukon Territory, Canada, since 1951. The lakes experienced a water deficit that is attributed to a warmer climate and less precipitation. Enhanced evaporation and an increase in EC were observed in ponds in the western Hudson Bay Lowlands studied by Wolfe et al. (2011). On Ellesmere Island in the Canadian High Arctic, Smol & Douglas (2007) witnessed in 2006 the temporary desiccation of ponds that had been permanent water bodies since 1983. The authors linked the desiccation to warmer air temperatures, less precipitation and, in turn, stronger evaporation.

Water stable isotopes in the 26 other ponds shifted to more negative values throughout the season. δ^{18}O shifted from -16 to $-14‰$ in late July to -18 to $-16‰$ in late August while δD shifted from -130 to $-120‰$ to about -150 to $-140‰$. Shifts towards more negative values cannot be explained by evaporation. As the dominant pond water supply source, summer precipitation needs to be taken into account. The Kytalyk study area experienced 18 rainfall days within the 48-day monitored time period. The individual water stable isotope values of local rainwater feeding the ponds varied by about 10‰ in δ^{18}O and by about 50‰ in δD which was considerably larger than the variation seen in the ponds. The water stable isotope composition of rainwater shifted from a δ^{18}O of $-12‰$ in July to $-22‰$ in August, and from a δD of $-110‰$ in July to $-160‰$ in August. Therefore, isotopic shifts are related to the recharge precipitation with lower water stable isotope composition. Isotopic shifts related to the input of melt water from ground ice are assumed to be of a minor extent.

In general, precipitation events are identified as the main drivers of water level fluctuations while air-temperature-induced evaporation also contributes to changes in pond water level. Small and shallow water bodies respond instantaneously to temperature fluctuations and changes in water supply, while the underlying permafrost allows surface depressions to accumulate water bodies and determines their morphology. Small periglacial water bodies and their hydrological regime are therefore particularly sensitive to changes in local meteorological and permafrost conditions.

Comparison to similar records

A comparison with similar studies of hydrochemical and limnological baseline characteristics (Hobbie 1980; Pienitz et al. 1997a, b; Duff et al. 1999; Hamilton et al. 2001; Michelutti, Douglas, Lean et al. 2002; Michelutti, Douglas, Muir et al. 2002) and ecological studies of ostracod assemblages (Wetterich, Herzschuh et al. 2008; Wetterich, Schirrmeister et al. 2008; Bunbury & Gajewski 2009) reveal a common pattern in the hydrochemistry of Arctic freshwaters (Supplementary Table S3). Corresponding to the mean pH of 6.3 of periglacial waters in the Indigirka Lowland, circumneutral to slightly alkaline pH values were found in circumarctic studies. On average, EC values between 100 and 380 µS cm^{-1} are reported from sites in the Arctic Canadian Archipelago, 70–220 µS cm^{-1} in northern Alaska (Hobbie 1980) and 205 µS cm^{-1} in the Moma region of northern Yakutia. In contrast, the major ion concentrations and EC are several orders of magnitude lower in periglacial freshwater bodies from the Indigirka Lowland and in the Lena River Delta. The low ion content of those water bodies results from the distance to the sea, bedrock geology and surrounding soils. Welch & Legault (1986) found high concentrations of sea salt that originated from sea spray and moderately acidic pH value in precipitation that feeds ponds and lakes at the western shore of Hudson Bay. For water bodies in the Moma region, assumed evaporation processes seem to be responsible for higher ion content. However, some Arctic ponds and lakes in the western Canadian Arctic are even more dilute, with a mean EC of 8.8 μS cm^{-1}. Those water bodies are located on Precambrian bedrock and coarse till, approximately 200 km from the Beaufort Sea and the western shore of Hudson Bay. Similar to the study area in the western Canadian Arctic, it is a distance of 100–200 km between the Laptev and East Siberian seas and study sites located on the Taimyr Peninsula, the Lena River Delta and Kytalyk in the Indigirka Lowland (Supplementary Table S3). Therefore, marine aerosols as a source of major ions can be largely ruled out. Hence, the dilute nature of the water bodies is related to summer precipitation as the dominant water source. The EC of the studied ponds in the Indigirka Lowland was close to the mean 22 μS cm^{-1} EC of rainwater collected in the Kolyma Lowland in summer 2012 (Schirrmeister, unpubl. data). The ionic composition and EC in precipitation over northern and central Canada was found to vary between the observation years (Schindler et al. 1976) and is known to vary in rain, with a mean EC of 8–10 μS cm^{-1}, and snow, with a mean EC of 14–40 μS cm^{-1} (Welch & Legault 1986). The water stable isotope composition of the ponds in this study and other small periglacial water bodies on the Arctic Siberian lowlands closely correspond to the isotopic composition of local rainwater. Consequently, rainfall plays a key role in the hydrochemical system of polygon ponds and other Arctic periglacial freshwaters (Prowse et al. 2006), despite its annual amount of only 354 mm.

Conclusions

We obtained freshwater ostracod assemblages and measured limnological characteristics of 27 polygon ponds and small periglacial water bodies from the Indigirka Lowland in north-east Siberia. A monitoring approach revealed the seasonal limnological variability of a typical low-centre polygon pond and its ostracod population. The following conclusions can be drawn from this study.

Abundant and diverse freshwater ostracods occur in polygon ponds and small periglacial water bodies of the Indigirka Lowland. Variability in species assemblages in different landscape units and pond types is small due to largely homogeneous habitat conditions.

The first finding of the freshwater ostracod species *Fabaeformiscandona groenlandica*, *F. krochini* and *Fabaeformiscandona* sp. in the Indigirka Lowland in north-east Siberia is reported in this study.

New insights in seasonal population dynamics as obtained for *Fabaeformiscandona pedata* represent baseline data about the largely unexplored life cycles of Arctic microcrustaceans.

River flooding influences the hydrochemical composition in substrate and water of ponds located in the Berelekh River floodplain. Among the different pond types, intrapolygon and interpolygon ponds differ in morphology and biogeochemical properties.

A monitoring approach reveals local meteorology to be the main driver controlling aquatic habitat conditions in small and shallow periglacial water bodies. Thus, these water bodies respond with particular sensitivity to changes in meteorological and permafrost conditions.

The close link between aquatic ecosystems in the Arctic, climate and permafrost underscores the importance of establishing detailed data sets in order to detect seasonal variability on different time scales and future environmental changes in the Arctic. Freshwater ostracods from permafrost areas are valuable biological indicators of aquatic environmental conditions and the atmospheric drivers influencing those conditions. Since permafrost deposits have a high preservation potential, fossil ostracod assemblages provide comprehensive insights into past environmental conditions, if recent reference data sets of limnological information and species records are available for comparison. This requirement highlights the need for further systematic studies of modern environmental dynamics and ostracod assemblages in the Arctic.

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