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PRIMARY RESEARCH PAPER

Spatial heterogeneity of the population age structure of the ostracode *Limnocythere inopinata* in Hulun Lake, Inner Mongolia and its implications

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Abstract Most existing studies of lacustrine ostracodes have been focused on species composition, and little attention has been paid to population structure. In this study, 39 surface-sediment samples from Hulun Lake, Inner Mongolia, were analyzed for ostracode species composition and 17 of them also for population structure of *Limnocythere inopinata*, which is the dominant ostracode in the lake. A total of nine ostracode species were recovered, most of which show high abundances at sites with rich plant detritus, implying the possible control of food supply on ostracode species occurrence in the lake. On the other hand, both the subfossil and the living populations of *L. inopinata* have greater numbers of early instars in deeper waters, while middle and late instars occur mostly in shallower waters, which is related to the grainsize composition of the substrate, denoting a hydraulic control on population structure. Pre- and post-mortem transport of ostracodes may be responsible for the observed within-lake changes in the population structure, although other factors such as migration, intrinsic population dynamics, and life cycle could also be involved. Our data provide insights into the interpretation of lake conditions when using ostracodes in paleolimnological research of lakes with similar natural settings.

Keywords Hulun Lake · Surface sediment · Ostracode · Population structure · Water depth · Taphonomy

Introduction

Ostracodes, microcrustaceans with low-Mg calcite shells, are ubiquitous in oceans, lakes, swamps, ponds, and rivers. They molt and subsequently regenerate a larger carapace when growing up, and most species produce eight pairs of juvenile valves and one pair of adult valves during their life. The valves of adults and different juveniles provide ideal materials for the research into limnological processes and regional environments (Schwalb et al., 1998; Alin & Cohen, 2003; Zhu et al., 2010). The modern occurrences of ostracodes in lakes of different salinities (Mourguiart & Carbonel, 1994; Mezquita et al., 2005; Reed et al., 2012) and different temperatures (Viehberg, 2006; Horne &

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Mezquita, 2008), as well as in different water depths (Mourguiart & Carbonel, 1994; Mischke et al., 2010) and areas with different organic debris content of the substrate (Jungwirth, 1979) and dissolved oxygen concentration in the bottom water (Martín-Rubio et al., 2005) have been extensively investigated in individual lakes to document the ecological characteristics of different ostracode species. The data obtained from such investigations have frequently been applied to interpreting variations in fossil ostracode assemblage of the sedimentary sequences of lakes (Mezquita et al., 2005; Mischke et al., 2008; Viehberg et al., 2008).

It is recognized that the ostracode instars of different growth stages possess quite different environmental preferences and capablilities (Van Doninck et al., 2003; Decrouy et al., 2012) due to differences in their body size and appendage structure (Snodgrass, 1956; Meisch, 2000). Therefore, even the same species of ostracodes may have different population age structures when living in different environments (Ruiz et al., 2003). It has been suggested that the age structure of an ostracode species may be informative of environmental conditions (Whatley, 1983, 1988). Until now, however, most studies of either extant or fossil ostracodes are still confined to analyses of the species composition. Little is known about the spatial distribution of extant ostracode in regards to the population age structure. There is a pressing need to investigate the distribution of different instars of ostracodes in modern lakes to improve the interpretations of past lake conditions based on ostracode data.

Lake Hulun in northeastern Inner Mongolia, China's fifth largest lake, is a good candidate for studying the within-lake changes in population structure of an ostracode because of its relatively low species diversity and high abundance. Wang & Ji (1995) collected the surface 2-cm sediments from five sites of Hulun Lake and investigated the species composition of ostracodes. Seven species of ostracodes were reported with *Limnocythere dubiosa* being the dominant one (Wang & Ji, 1995). Ever since then, little attention has been paid to the ostracodes of Hulun Lake. In this study, we analyzed the species composition and age structure of the ostracodes from 39 surface-sediment samples taken along two transects in Hulun Lake. We attempt to investigate the occurrence of different instars of the dominant ostracode in the lake and examine the differences among different species and different instars of the same species. The aim of this study is to reveal the relationship between the spatial distribution and the age structure of the ostracodes in the lake and the lacustrine environment. This study will not only improve our understanding of the taphonomy and ecology of lacustrine ostracodes but will also have valuable implications for reconstructing the hydrological history of lakes based on data from lake sediment cores.

Study site

Hulun Lake (48°30.667′ to 49°20.667′N, 117°0.167′ to 117°41.667′E), also known as Dalai Lake, is the fifth largest lake in China and lies in an inland graben basin in Inner Mongolia (Fig. 1). It has an area of 2,339 km^2 and a maximum water depth of 8 m when the lake level is 545.3 m above sea level (a.s.l.; measurements taken in August 1964; Xu et al., 1989). In the 1980s and 1990s, the lake level fluctuated between 544 and 545 m a.s.l. with the maximum water depth ranging from 7 to 8 m (Li et al., 2007). During the last decade, the lake has contracted continuously and the maximum water depth dropped to 3.15 m in August 2009.

According to our measurements taken in August 2009, the bottom water of Hulun Lake had a pH of 9.2 and a salinity of 2.5 g l^{-1} and contains major cations of Na^+ (81.9%), K^+ (1.8%), Mg^{2+} (13.7%), and Ca^{2+} (2.6%) and major anions of HCO_3^- (52.8%), CO_3^{2-} (9.4%), Cl^- (23.5%), and SO_4^{2-} (14.4%). The temperature of the bottom water is around 19.3°C, and the dissolved oxygen content approximates 6.5 mg l^{-1}. The bottom water shows minor differences in the above parameters within the lake at the time of measurement.

Aquatic plants are scarce in the lake and confined to the areas of the river mouth and parts of the littoral zone. The benthic fauna living in the lake today consists mainly of Oligochaeta, Gastropoda, Bivalva, Hirudinea, Crustacea, and Insecta, and most of these animals generally inhabit the northern part of the lake (Xu et al., 1989).

Low mountains and hills of Mesozoic volcanic rocks border the lake on the northwest and form a northeast–southwest trending fault-scarp shoreline. Broad lacustrine and alluvial plains scattered with eolian dunes are present along the southern and eastern shore of the lake. The lake has a catchment of 37,214 km^2 within the borders of China. Two major rivers, the Herlun and Urshen Rivers, enter the lake from the southwest and southeast (Fig. 1). The Dalanolom River, an intermittent river to the northeast of the

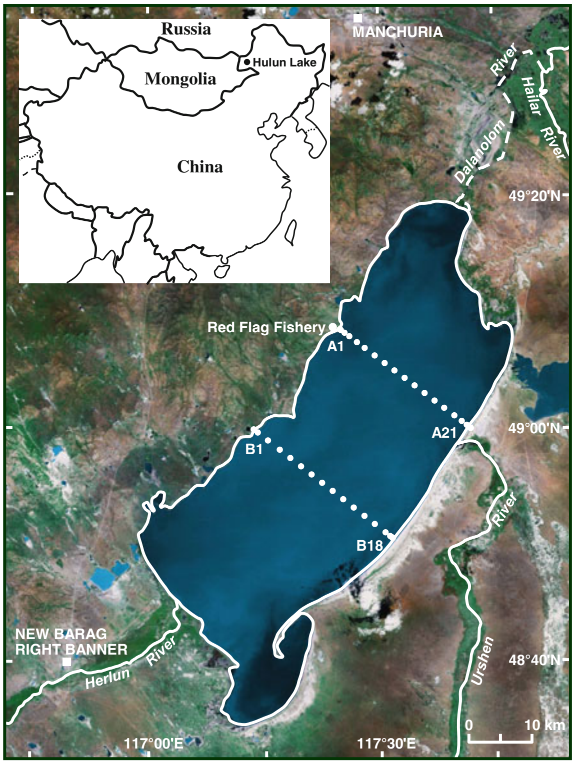


Fig. 1 Map of Hulun Lake (from http://maps.google.com) showing locations of the surface-sediment sampling sites along the transects A and B. The inset gives a sketch map of China showing the location of Hulun Lake

lake, connects the lake with the Hailar River. It flows into the lake when the lake level is lower than the water level in Hailai River, and drains the lake when the lake level is higher than the water level in Hailai River (Xu et al., 1989; Fig. 1).

Hulun Lake is located in a semi-arid area of the middle temperate zone (Chinese Academy of Sciences, 1984; Xu et al., 1989). In the lake region, mean annual temperature is 0.3°C with a July average of 20.3°C and a January average of −21.2°C. Annual precipitation varies from 247 to 319 mm, and more than 80% of it falls in June–September. Annual evaporation reaches 1,400–1,900 mm, which is five to six times the annual precipitation. The lake is covered with ca. 1 m of ice from November to April (Xu et al., 1989; our field observations).

The modern natural vegetation of the Hulun Lake basin is categorized as middle temperate steppe and is dominated by grasses and *Artemisia* species (Compilatory Commission of Vegetation of China, 1980; Xu et al., 1989). The vegetation cover ranges from relatively moist forb-grass meadow-steppe in the piedmont belt to moderately dry grass steppe on the alluvial plain and dry bunchgrass–undershrub *Artemisia* steppe on the lacustrine plain. Halophilic Chenopodiaceae plants are developed in the lowlands. Small patches of open elm forests and sandy shrubs grow in the stabilized dune fields. Tall-grass meadows can be seen in the river valleys.

The lake region is sparsely populated. Local people are engaged in animal husbandry and fishery and do not undertake any agricultural activity. The Inner Mongolian Fishery Company was set up in 1948 to organize fishery production, and several fishery units had been formed along the lake during the subsequent decade. Since the 1990s, fishery management activities have only been implemented in winter to protect fish resources (Xu et al., 1989).

Materials and methods

Surface-sediment sampling

The surface sediments of Hulun Lake were sampled in late August 2009 along two northeast–southeast transects A and B, yielding 21 samples for transect A and 18 samples for transect B (Fig. 1; Table 1). At each sampling site, a sediment core was retrieved in either a 40- or 60-cm-long polyethylene tube with an inner diameter of 70 mm (ca. 38.5 cm^2) using a gravity corer. The water–sediment interface and millimeter-scale thick whitish-gray deposits on the sediment top were clearly discernible in the core tube. The top 1 cm (ca. 38.5 cm^3) of each core section was cut for a sample of the surface sediments after siphoning the water out of the core tube with a plastic pipe. The top 1 cm of the surface sediments approximately covers the last 30 years as estimated with the age–depth model for the HL06 sediment core retrieved from the deepest part of the lake (Xiao et al., 2009). About 1 ml of each sample was stored in 70% ethanol for analyses of living ostracodes. The water depth and offshore distance of each sampling site were measured at the time of extraction (Table 1).

Analyses of ostracode assemblage

The analysis of subfossil ostracodes was carried out separately using 0.1 g of dry sediment for the

Table 1 Water depth and offshore distance of 39 surface-sediment sampling sites along transects A and B in Hulun Lake (measurements in August 2009)

Sample number	Water depth (m)	Offshore distance (km)
A1	0.70	0.02
A2	1.00	0.05
A3	1.60	1.26
A4	2.10	1.00
A5	2.45	1.88
A6	2.85	3.45
A7	2.95	5.00
A8	3.00	7.00
A9	3.10	9.00
A10	3.15	11.00
A11	3.05	13.00
A12	3.00	11.30
A13	2.90	9.30
A14	2.90	7.30
A15	2.85	5.30
A16	2.55	3.30
A17	2.15	1.80
A18	1.60	0.80
A19	1.10	0.30
A20	0.65	0.10
A21	0.40	0.02
B1	1.00	0.06
B2	1.45	0.23
B3	1.95	0.82
B4	2.35	2.80
B5	2.75	5.00
B6	2.85	7.00
B7	2.85	9.00
B8	2.85	11.00
B9	2.85	13.00
B10	2.85	12.10
B11	2.85	10.10
B12	2.85	8.10
B13	2.80	6.10
B14	2.55	4.10
B15	2.25	2.10
B16	1.75	1.20
B17	1.25	0.90
B18	0.80	0.70

dominant species, *L. inopinata*, and 1 g for the less abundant species. The extraction of subfossil ostracode valves follows the method described by Zhai et al. (2010). For each sample, 60 ml of 10% H_2O_2–0.1% Na_2CO_3 solution (pH 9–10) was added to disaggregate the sediment for 24 h. The resulting residue was sieved in water through a 63-µm mesh. The sieve residue was rinsed repeatedly, spread onto some glass plates (9×12 cm^2) as thin stripes with a pipette (4-mm inner-caliber) and then dried at 40°C. All the ostracode valves extracted from the samples were identified and counted with an Olympus stereomicroscope (using magnifications between 40× and 100×). Following this procedure, the valves of both living and dead individuals were counted up together without discrimination.

The extraction and dissection of living ostracodes followed the methods of Tressler (1959) and Meisch (2000). For each sample, the wet sediment stored in ethanol was sieved in water through a 63-µm mesh, and the sieve residue was transferred to a Petri dish. Intact carapaces were picked out under an Olympus stereomicroscope, and each of them was put into a small drop of Hydro-Matrix® on a glass slide. The valves were removed with a pair of insect needles and kept in a micropalaeontological slide after Hydro-Matrix was rinsed away with clean water. Sometimes, especially for small individuals, the valves were decalcified and softened by Hydro-Matrix, and were sealed together with the soft parts without being picked out and stored dry. The soft parts were dissected and covered with a glass slice for the examination with an Olympus compound microscope at 100× or 400× magnification. Only specimens with well-preserved soft parts were counted.

The identification of the ostracodes follows the taxonomy of Martens (1991), Victor & Fernando (1981), Janz (1994), Meisch (2000), and Hou et al. (2002). Most of the ostracodes were identified by shell morphology. For the genus *Ilyocypris*, however, characteristics of the soft part were also considered due to less difference in the shell morphology of the different species in this genus.

Analyses of population age structure of *L. inopinata*

The population age structure of *L. inopinata* was analyzed for both the subfossil populations and the living ones. The valve length of *L. inopinata* from the samples was measured, and a frequency distribution with respect to different instars was generated. From the length distribution, different cohorts were recognized and identified as representing the A-8 (the youngest) through the A (the adult) stages of *L. inopinata*. Meanwhile, detailed observations were made on the soft parts of the living specimens, and the observed successions in limb and chaetotaxy structure were compared with Smith & Kamiya (2003) (on *Loxoconcha japonica*) to confirm and adjust the above scheme of length-based division of life stages. Finally, the instar stages of subfossil valves and living individuals of *L. inopinata* from the selected samples were determined by measuring the length of valves/carapaces. For broken valves, the lengths of which cannot be measured directly, dimensions other than lengths were measured and the lengths were calculated for stage determination (see Fig. S1 in Electronic Supplementary Material). The A-1 and A instars were distinguished by the presence of radial pore canals on the marginal zone of the A instar in view of an overlap in the valve length of both.

Analyses of substrate plant fragment and grainsize

Plant fragments in a sample were counted, if present, in the course of counting the subfossil ostracodes. The abundance of plant fragments in the sample was graded into five levels: (1) very rare (<10 pieces g^{-1}), (2) rare (10–50 pieces g^{-1}), (3) moderate (50–100 pieces g^{-1}), (4) abundant (100–500 pieces g^{-1}), and (5) very abundant (>500 pieces g^{-1}).

Grain-size distribution of the surface-sediment samples was determined with a Malvern Mastersizer 2000 laser grain-size analyzer (Xiao et al., 2012). About 200 mg of sediment from each dry sample was pretreated with 10–20 ml of 30% H_2O_2 to remove organic matter and then with 10 ml of 10% HCl with the sample solution boiled to remove carbonates. About 2,000 ml of deionized water was added, and the sample solution was kept for 24 h to rinse acidic ions. The sample residue was dispersed with 10 ml of 0.05 M $(NaPO_3)_6$ on an ultrasonic vibrator for 10 min before grain-size analysis. The Mastersizer 2000 has a measurement range of 0.02–2,000 μm in diameter and a grain-size resolution of 0.166 phi in interval, thus yielding 100 grain-size fractions. It automatically outputs the median diameter (Md, the diameter at the 50th percentile of the distribution) and the volume percentages of clay (<2 μm), silt (2–63 μm), and sand (63–2,000 μm) fractions of a sample. The relative error is <1% on the 50th percentile and 2% on the outlying percentiles.

We use Md to represent the sediment texture in general. On the other hand, the grainsize was divided into five fractions, namely, the <32, 32–63, 63–125, 125–250, and the >250 μm fractions, to study the relation between the population structure of *L. inopinata* and the substrate grainsize in more detail.

Numerical analyses

The method of Constrained Incremental Sum of Squares (CONISS, Grimm, 1987) was used with the program Tilia 1.7.16 to divide the ostracode-abundance diagram of 39 surface-sediment samples from Hulun Lake into ostracode-assemblage zones. Moreover, the program CANOCO 4.5 (Ter Braak & Šmilauer, 2002) was used to ordinate the ostracode data from the samples and to detect the pattern of spatial distribution of the ostracodes and the relation between the ostracodes and the environmental variables. The abundance data for ostracode taxa with occurrences in at least five samples, as well as the percentage data of the A-7 instar to the adult of *L. inopinata*, were used for ordination in ordination with a square root transformation. The content of sand (63–2,000 μm) and the abundance of plant fragments in the samples were selected as the environmental variables. Detrended correspondence analysis (DCA) showed that the gradient length of the first axis is 0.452 for the species abundance data, and is 1.383 for the age-structure data of *L. inopinata*, indicating a linear response of the ostracodes to the environmental variables (Ter Braak & Šmilauer, 2002). Therefore, redundancy analysis (RDA) was chosen for ordination of the ostracode data and the environmental variables (Ter Braak & Šmilauer, 2002). Partial RDA was used to examine the effect of each environmental variable on the ostracodes, and Pearson correlation coefficients were calculated among the five grainsize fractions, the plant fragment content, the abundance of *L. inopinata*, and the percentages of the species' instars as well as the mean population stages of the samples. The overall objective was to study the relation between the ostracode's population structure and the environments, as well as the dependence of population structure on abundance.

Results

Within-lake distributions of ostracode species

The surface sediments of Hulun Lake contain abundant ostracodes. A total of 27,890 valves were counted from 39 dry samples, and in most samples the abundance ranged from 300 to 20,000 valves g^{-1}. A total of 245 living individuals were obtained from the 17 selected wet samples, and the abundance of the ostracodes in the samples varies from 2 to 64 individuals ml^{-1}. Nine species of ostracodes belonging to eight genera were found. These included *L. inopinata* (Baird), *Ilyocypris* sp., *Pseudocandona* sp., *Candona* sp., *Candoniella mirabilis* Schneider, *Plesiocypridopsis* spp., *Darwinula stevensoni* Brady & Robertson, and *Notodromas* sp., with *L. inopinata* representing 96.9% of the total community (Figs. 2, 3). Living ostracodes in the lake were also dominated by *L. inopinata* with a few *Ilyocypris* sp. Living individuals of the other species were not detected in this study.

Limnocythere inopinata occurred as an asexual population, and most of the specimens were unnoded. Adult *Ilyocypris* sp. bears 5 + 1 swimming setae on the second antenna. The 1st–5th setae are sub-equal in length and extend beyond the terminal claws by ca. 50% of the total length; whereas, the 6th one extends only to the middle part of the terminal claws. The walking legs are five-segmented. The hemipenis has four distal lobes. The “Zenker” organ bears 17–21 rings. The posterior inner lamella of the left valve has 11–14 marginal ripplets (Fig. 2B). The *Ilyocypris* sp. found in Hulun Lake has different morphological features from the *Ilyocypris* species described in existing literatures, and was thus identified as *Ilyocypris* sp. in this study. The *Plesiocypridopsis* in the lake actually includes two morphotypes, one of which has smaller pits and more detectable reticula on the valve surface than the other (Fig. 2B). These features of the *Plesiocypridopsis* are only discernable with the SEM, and the two types were therefore recorded as *Plesiocypridopsis* spp. in this study (Fig. 3).

According to CONISS, the abundance diagrams of subfossil ostracodes for transects A and B were each divided into two ostracode-assemblage zones with four subzones, i.e., 1a, 1b, 2a, and 2b from the northwestern shore to the southeastern shore of the lake (Fig. 3). These subzones displayed considerable variation both in the species composition and in the abundance of the ostracodes. In transect A, the ostracodes showed low abundance and poor diversity in subzone 1a with the presence of only a few *L. inopinata* and *Ilyocypris* sp. In subzone 1b, both *L. inopinata* and *Ilyocypris* sp. increased, and *Pseudocandona* sp. also occurred, resulting in peak values of the ostracode abundance in the area with water depths of 1.60–2.45 m. In subzone 2a, *L. inopinata*, *Ilyocypris* sp., and *Pseudocandona* sp. were abundant, and *Candona* sp., *C. mirabilis*, *Plesiocypridopsis* spp., and *D. stevensoni* occurred frequently. The abundance of ostracodes decreased obviously in subzone 2b except for sample A21, which had the highest abundance (20,892 valves g^{-1}) of ostracodes among all the samples. Several ostracode species occurred in this sample, and all showed high abundances.

In transect B, subfossil ostracodes were abundant and diverse in subzone 1a with *L. inopinata*, *Ilyocypris* sp., and *Pseudocandona* sp. being accompanied by *Plesiocypridopsis* spp. and *D. stevensoni*. Both the abundance and the diversity of ostracodes decreased significantly in subzone 1b. In subzone 2a, *L. inopinata*, *Ilyocypris* sp., and *Pseudocandona* sp. were abundant, and *Candona* sp., *C. mirabilis*, and *Plesiocypridopsis* spp. occurred frequently, leading to an average abundance of 13,160 valves g^{-1}, the highest average abundance among all the subzones. In subzone 2b, the ostracode abundance and diversity decrease to some extent as compared with that of subzone 2a. Overall, the abundance and diversity of the ostracodes were higher in the southeastern than in the northwestern part of Hulun Lake. Most of the ostracode species attained their maximum abundances in the zone between water depths of 2 and 3 m.

Population structure of *L. inopinata*

The population age structure of the dominant species, *L. inopinata*, was analyzed based on the lengths of valves in 17 samples. The valve length of *L. inopinata* has a polymodal distribution, indicating that different cohorts represent different development stages of the species (Fig. 4; Table 2). Except for the A-8 juveniles, the youngest instar, which were only obtained in small numbers, all instars were recovered abundantly (Fig. 4). The low number of A-8 instars may have resulted from the low preservation potential of the poorly calcified, soft carapace of this instar. In the

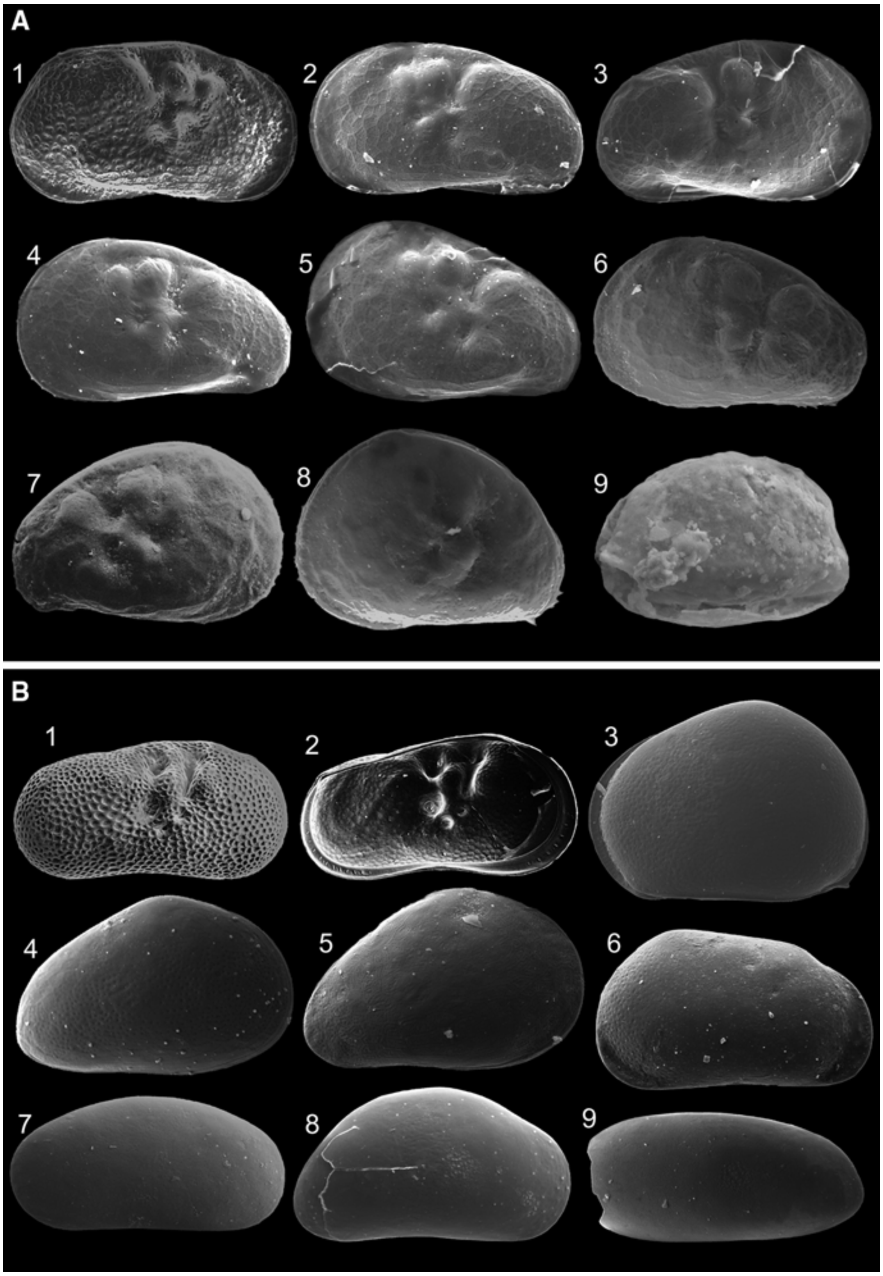


Fig. 2 Photos of ostracodes in the surface sediments of Hulun Lake, generated by a Zeiss EVO® 18 scanning electron microscope. **A** *Limnocythere inopinata* (Baird): *1* female adult, RV, 460 × 260 µm; *2* A-1 instar, LV, 420 × 235 µm; *3* A-2 instar, RV, 330 × 195 µm; *4* A-3 instar, LV, 285 × 170 µm; *5* A-4 instar, LV, 225 × 140 µm; *6* A-5 instar, LV, 190 × 120 µm; *7* A-6 instar, RV, 160 × 105 µm; *8* A-7 instar, LV, 120 × 90 µm; *9* A-8 instar, carapace in right view, 100 × 75 µm. **B** other species. *1 Ilyocypris* sp., male adult (judged from the soft part), RV, 690 × 350 µm; *2* male adult (judged from the soft part), LV, 735 × 380 µm; *3 Notodromas* sp., female adult, LV, 995 × 730 µm; *4 Plesiocypridopsis* sp. 1, juvenile, RV, 300 × 195 µm; *5 Plesiocypridopsis* sp. 2, juvenile, RV, 280 × 180 µm; *6 Pseudocandona* sp., female adult, RV, 855 × 495 µm; *7 Candoniella mirabilis* Schneider, juvenile, RV, 445 × 220 µm; *8 Candona* sp., juvenile, RV, 490 × 275 µm; *9 Darwinula stevensoni* Brady & Robertson, late juvenile, RV, 510 × 240 µm. RV Right valve; LV left valve

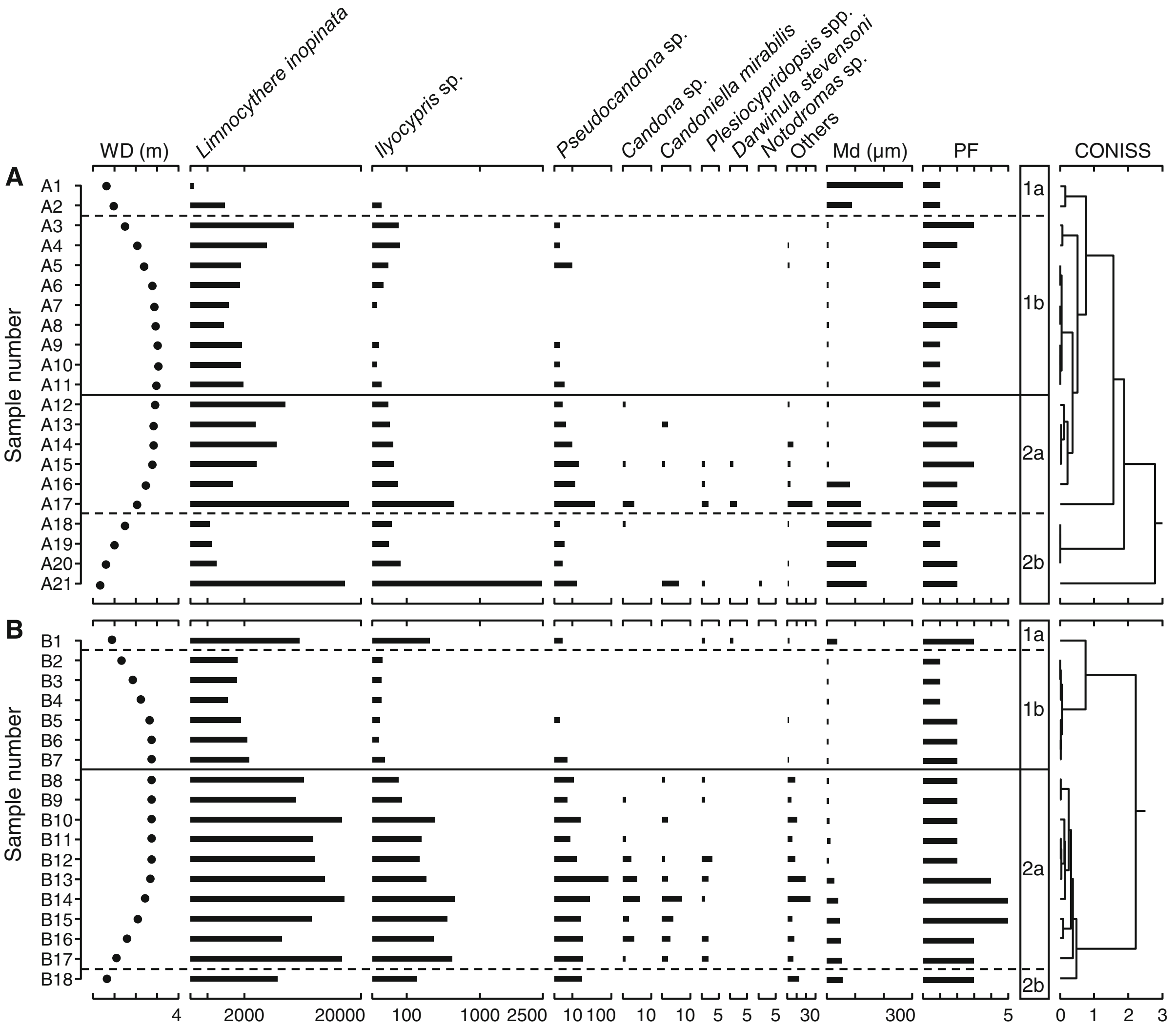


Fig. 3 Water depth (WD, m) of the sampling sites and abundance (v g^{-1}) of the ostracodes, median diameter (Md, the diameter at the 50th percentile of the distribution) of the substrate, abundance of the plant fragments (PF) in 39 samples of the surface sediments from Hulun Lake. **A** transect A, **B** transect B. The abundances of *L. inopinata*, *Ilyocypris* sp., and *Pseudocandona* sp. are expressed on square root scales. PF is expressed as five scales with the lowest (1) and the highest (5) indicating <10 and >500 fragments g^{-1} sediments, respectively. Cluster analysis (CONISS) is based on the total sum of squares ($\times 10^4$)

following descriptions and discussions, we will focus on the A-7 to the A instars.

The population structure of the subfossil *L. inopinata*, presented as percentage histograms of the nine stages, displayed significant spatial heterogeneity across the lakebed (Fig. 6). In deeper parts of the lake (samples A5, A9, A12, A13, B5, B8, B9, B12, and B13 from depths > 2 m, as well as A3 from a depth of 1.60 m), the subfossil populations were dominated by the early juveniles (A-7 and A-6), with decreasing numbers of the later instars in each. By contrast, in shallower parts of the lake (samples A16, A17, A19, A21, B1, B16, and B17), the subfossil populations of *L. inopinata* were dominated by the middle or late instars, and displayed a more or less unimodal population structure. As the water became shallower, the samples became dominated by increasingly advanced instars. In other words, the subfossil *L. inopinata* in Hulun Lake showed younger populations in deeper waters and older populations in shallower waters.

The instar composition of living *L. inopinata* was also analyzed to provide information on the population

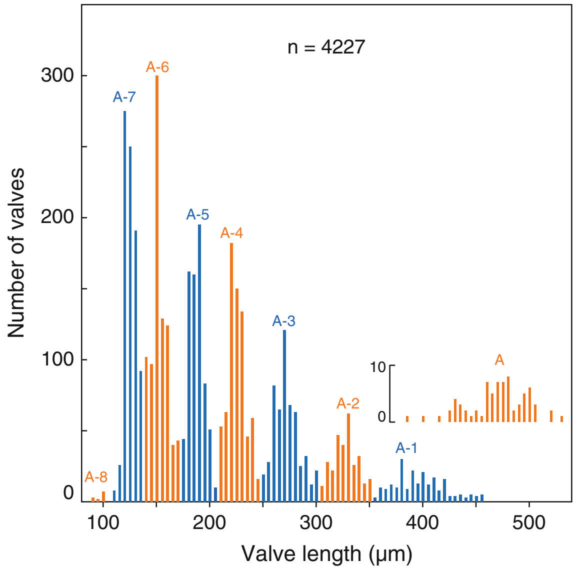


Fig. 4 Frequency distributions of valve lengths of the A-8 to A instars of *L. inopinata* in the surface sediments of Hulun Lake. The valve lengths were direct measurements obtained with an Olympus stereomicroscope at 100× magnification. Note the different scale applied to the adult. Also see Table 2

Table 2 Lengths of valves of the A-8 to A instars of *L. inopinata* in the surface sediments of Hulun Lake

Instar	Valve length (μm)
A-8	90–100
A-7	110–135
A-6	140–170
A-5	175–205
A-4	210–245
A-3	250–300
A-2	305–350
A-1	355–455
A	385–530

Also see Fig. 4

structure during the season in which sampling occurred (Fig. 6). Owing to the low number of living individuals, it is difficult to know the exact population structure in most samples. Nonetheless, some samples (e.g., A5, A12, A13, B5, and B8) from deeper parts of the lake exhibited a weak dominance by the middle instars. By contrast, an obvious dominance by late juveniles and adults was found in shallower waters (e.g., samples A21, B13, and B16). In sample A21, most of the recovered individuals were adults, forming a rather old population.

Comparisons were made between the spatial change in the mean population stage of the subfossil population and that of the living population (Figs. 6, 8). Both displayed a pattern of younger populations in the lake center and older populations in the littoral zone. However, the mean population stage of the living population was older than that of the subfossil population in most samples (Fig. 8).

Substrate plant-fragment abundance and grain-size composition

Plant fragments in the surface sediments of Hulun Lake displayed dramatic variations in the abundance ranging from <10 pieces g^{-1} of dry sediment (grade 1, very rare) up to >500 pieces g^{-1} (grade 5, very abundant) (Fig. 3). The abundance of plant fragments attained grade 4 (100–500 pieces g^{-1}) or 5 (>500 pieces g^{-1}) in the samples from the subzones 2a and 2b of both transects. In other words, plant fragments were more abundant in the surface sediments of the southeastern lake than in those of the northwestern lake.

All the surface-sediment samples of Hulun Lake consisted of particles finer than 2 mm, and no gravels (>2 mm) were found. As shown in Fig. 3, the Md of the substrate varied from 6 to 267 μm. In the littoral and sub-littoral zones of the lake, the Md was larger than 20 μm and decreased with increasing water depth (Fig. 3). Sediments in these areas were represented by various size fractions, ranging from the <32 μm fraction to the >250 μm fraction (Fig. 6). In the relatively flat lakebed of the central lake, the Md was less than 20 μm and displayed little change. Sediments from these sites were dominated by fine particles <32 μm with few coarser grains.

Results of RDA and partial RDA

RDA of the major ostracode taxa from the surface-sediment samples and environmental variables showed one strong relationship between the ostracode abundance and the selected environmental variables (Fig. 5). The first axis of RDA captured 38.1% of the total variance within the ostracode data and was positively related to the plant-fragment abundance; whereas the second axis captured only 0.9% of the

Fig. 5 RDA biplot of six ostracode taxa with occurrences in at least five samples and the two environmental variables (median diameter of the substrate and abundance of the plant fragments in the surface-sediment samples)

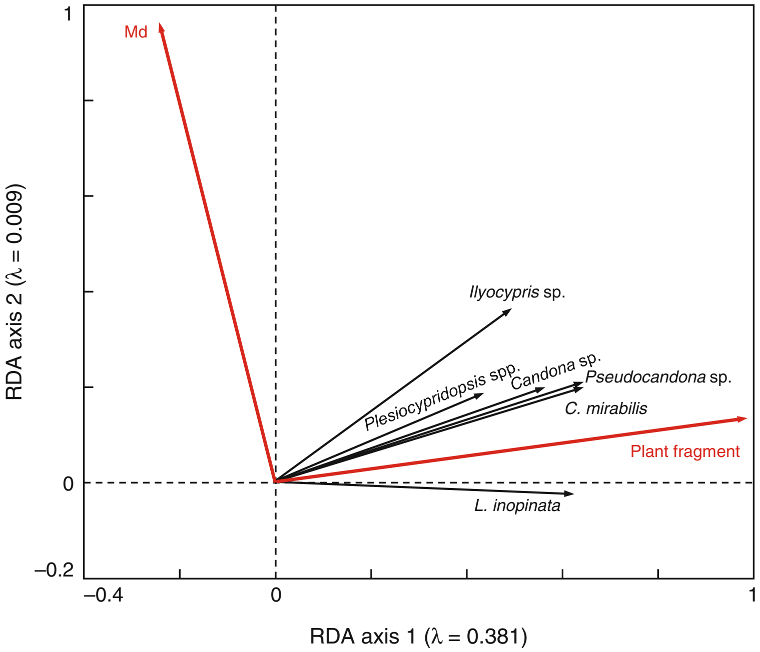


Table 3 Partial RDA of the abundances of six ostracode taxa with occurrences in at least five samples from the surface sediments of Hulun Lake

Variable	Covariables	λ_1	λ_1/λ_2	Significance (P)	Variance (%)
Md	PF	0.016	0.027	0.322	2.6
PF	Md	0.359	0.602	0.002	37.1

The median diameter (Md) and abundance of the plant fragments (PF) in the samples are used as variable or covariable separately

total variance and was related positively to Md. All the arrows of the ostracodes were positioned in the positive direction of the first axis, i.e., they were close to the direction of the plant-fragment abundance but nearly vertical to that of Md. Partial RDA indicated that the plant-fragment abundance would have more influence on ostracode species occurrence in Hulun Lake than Md (Table 3).

On the other hand, the RDA of the subfossil *L. inopinata* instar percentages and environmental variables revealed a different relationship between the ostracode's population age structure and the environment (Fig. 7). The first axis of RDA captured 69.6% of the total variance within the age-structure data and was related positively to the 63–125 and the 125–250 μm grainsize fractions, and negatively to the <32 μm grainsize fraction. The second axis captured 11.7% of the total variance and was negatively related to the plant-fragment abundance and the 32–63 μm grainsize fraction. The instars of *L. inopinata* were generally arranged in an anti-clockwise order in Fig. 7, accompanied by a general increase in the grainsize of the substrate fractions (except for the >250 μm fraction).

Correlations between instars of *L. inopinata* and grainsize fractions of the substrate

Table 4 shows the results of the Pearson correlations between percentages of the instars of *L. inopinata* and the environmental variables. It is clearly seen that the percentages of the earlier juveniles, i.e., the A-7 through the A-5 instars were positively correlated with the percentage of finest soil fraction, while being negatively correlated with the coarser fractions. By contrast, the later instars, including the A-4 instar through the adult, were negatively correlated with the percentage of the finest sediment fraction, and in general positively correlated with the coarser fractions. The 32–63 μm grainsize fraction showed no significant correlation with the instars with the exception of a positive correlation with the A-4 instar. The >250 μm grainsize fraction was negatively related to the A-7 instar while positively related to the A-4 and the A-3 instars. The above relations, in general, resulted in a positive correlation between the

Table 4 Pearson correlation matrix, showing the correlations between the percentages of the A-7 instar through the adult, as well as the mean population stages of the subfossil populations of *L. inopinata*, and percentages of the five grainsize fractions, the abundance of the plant fragments (PF) as well as the abundance of *L. inopinata* in 17 surface-sediment samples from Hulun Lake

	A-7	A-6	A-5	A-4	A-3	A-2	A-1	A	Mean stage
<32 μm	.947†	.861†	.504*	−.591§	−.742¶	−.630¶	−.515§	−.629¶	−.858¶
32–63 μm	−.478	−.297	.256	.691†	.447	.011	−.076	−.030	.206
63–125 μm	−.936¶	−.873¶	−.493§	.537*	.730†	.659†	.539*	.633†	.867†
125–250 μm	−.673¶	−.741¶	−.805¶	.001	.419	.687†	.757†	.840†	.841†
>250 μm	−.498§	−.419	−.367	.488*	.484*	.392	.065	.179	.391
PF	−.152	−.039	.451	.359	.135	−.253	−.158	.007	−.020
Abundance	−.415	−.342	−.073	.319	.439	−.099	.197	.494*	.348

* Positive correlation, $P < 0.05$

† Positive correlation, $P < 0.01$

§ Negative correlation, $P < 0.05$

¶ Negative correlation, $P < 0.01$

mean development stage of the population and the coarser grainsize fractions and a negative correlation with the finest grainsize fraction.

Plant fragment content had no significant effect on which instars of *L. inopinata* present. Finally, it was found that the population structure is generally independent of the abundance of the species, except for a weak relation between the abundance and the adult percentage (Table 4).

Discussion

Relation between the ostracode species occurrence and the lake environment

Previous investigations indicate that the distribution of ostracodes in lakes is controlled by various environmental factors such as the coverage of aquatic plants on the lakebed (Mischke et al., 2010), the contents of organic detritus (Jungwirth, 1979) in the substrate, the grainsize of the sediment (Zhai et al., 2010), and the concentration of dissolved oxygen in the bottom water (Martín-Rubio et al., 2005; Curry & Filippelli, 2010), although the dominant factor varies from lake to lake. In Lake Donggi Cona (northeastern Tibet), where the maximum water depth is over 80 m, the ostracodes display a zonal within-lake distribution that is closely related to the presence of aquatic plants and the gastropod *Gyraulus* at different water depths (Mischke et al., 2010). In Lake Caisedo de Yuso in Spain, both the diversity and the abundance of ostracodes decrease obviously in the zone below a water depth of 10 m because of decreased dissolved oxygen and increased carbon dioxide in the bottom waters (Martín-Rubio et al., 2005). In Dali Lake in Inner Mongolia, the ostracodes are abundant and diverse in the intermediate zone between water depths of 7 and 9 m but scarce in the lake-center zone below a water depth of 10 m (Zhai et al., 2010). Such a distribution of the ostracodes in Dali Lake was interpreted to result from changes in the hydraulic dynamics of the lake water and the grainsize of the substrate across the lakebed (Zhai et al., 2010). In Lake Neusiedlersee, a large, shallow saline lake on the Austria–Hungary border, *L. inopinata* is much more abundant in the western littoral zone than in the other parts of the lake because a number of rivers bring organic detritus into the western part of the lake. This denotes a close relationship between the abundance of *L. inopinata* and the supply of organic detritus (Jungwirth, 1979).

Hulun Lake is a large and shallow lake with an area of over 2,000 km^2 and a maximum depth of about 3 m. All the ostracodes in the lake reach their maximum abundances in the sub-littoral and littoral zones of the southeastern lake where plant fragments are rich in the surface sediments (Fig. 3). The data of RDA and partial RDA suggest that the content of plant fragments in the substrate can be a key factor that controls the abundances of the ostracodes including the dominant species, *L. inopinata* (Fig. 5; Table 3). Ostracodes live on certain types of food, such as organic detritus and algae (Liperovskaya, 1948; Schmit et al., 2007). We thus infer that the terrestrial plant-fragment input into the lake from the catchment may have affected the propagation of the ostracodes in Hulun Lake, where macrophytes are rare (Xu et al., 1989), as a primary source of foods. Along the southeastern shore of Hulun Lake, broad lacustrine and alluvial plains are distributed where dry grass steppe and bunchgrass–undershrub steppe are developed. The Urshen River (and probably other surface flows as well) traverses through the plains into the lake (Fig. 1) and supplies the lake with terrestrial plant detritus, thus providing sufficient nutrients for the propagation of ostracodes in the southeastern littoral and sub-littoral zones.

It is noted that *L. inopinata* dominated the ostracode community in Hulun Lake. It is a ubiquitous species that occurs in many fresh–brackish water bodies in Eurasia (Yin et al., 1999; Van der Meeren et al., 2010), with a maximum salinity tolerance of 46 g l^{-1} (Yin et al., 1999). The success of *L. inopinata* in these habitats may be attributed to its ability to tolerate changes in salinity and alkalinity of water and to withstand other variations in the regional environment.

Possible mechanisms for the spatial heterogeneity of the population age structure of *L. inopinata*

Previous studies on the population age structure of subfossil ostracodes have been mainly undertaken in the coastal marine environments (Whatley, 1983, 1988; Ruiz et al., 2003). Based on investigations on the age structure of the subfossil ostracodes, such as Paradoxostomatidae and Xestoleberidae species, from the coastal sediments of England, Whatley (1983, 1988) found a spatial pattern of later stage instars in shallow waters and earlier stage instars in deep waters. Whatley proposed that the size-sorted distribution of ostracode valves in the coastal area is mainly caused by post-mortem transport. According to this hypothesis, smaller valves in the death assemblage are washed away from shallower waters to deeper waters, resulting in different age structures in different energy regimes. A similar spatial pattern of instar distribution was found for subfossil *Pontocythere elongata* in the surface coastal sediments of southwestern Spain (Ruiz et al., 2003), although those authors argued that this would have resulted from the natural growth of the ostracodes rather than the post-mortem modification by hydrodynamic processes.

The population structure of subfossil *L. inopinata* at Hulun Lake displays a spatial pattern that resembles those of marine ostracodes investigated by Whatley (1983, 1988) and Ruiz et al. (2003). In the littoral zone (e.g., sample A21; Fig. 6A), the population contains a large number of late instars with very few early instars. In the intermediate depths (e.g., samples A17 and B17), the population is dominated by middle instars. In the lake center (e.g., samples A9 and B9), the population contains a large number of early instars with very few advanced specimens. The distribution of different instars of *L. inopinata* matches the within-lake hydrodynamic gradient, with different instars associated with certain grainsize fractions of the substrate (Fig. 7; Table 4). It is also noted that in the southeastern part of the lake, where sediment grainsize displays a larger spatial gradient compared with the northwestern lake, the spatial changes in the population structure are also larger (Fig. 8). The observed size-sorted pattern in Hulun Lake seems to be best explained by post-mortem transport, as in the aforementioned marine ostracodes. However, observation on the living population of *L. inopinata* suggests that there may be other explanations for this spatial pattern.

As shown in Figs. 6 and 8, living populations of *L. inopinata* in the sampling season (i.e., late August) exhibited a spatial pattern of more advanced instars in shallower waters and earlier juveniles in deeper waters, which is similar to the distribution of the subfossil instars in the sediments. Moreover, the trend and magnitude of spatial changes in the living populations match those found in the subfossil populations, although the age structure of the living populations was consistently more advanced than that of the subfossil ones (Figs. 6, 8) due, probably, to seasonality. As found in former studies (Geiger et al., 1998), the early instars of *L. inopinata* emerge in April or May and most of them accomplish the development before October–November. So it is expected that the population structure in late August would be more advanced than the annual average state documented by the subfossil. Our data indicate that a spatial contrast in the age structure may have already been established before the populations die. This suggests that, the observed size-sorted distribution of *L. inopinata* instars in Hulun Lake would have been, at least to a considerable extent, caused by pre-mortem processes, although post-mortem transport cannot be excluded totally.

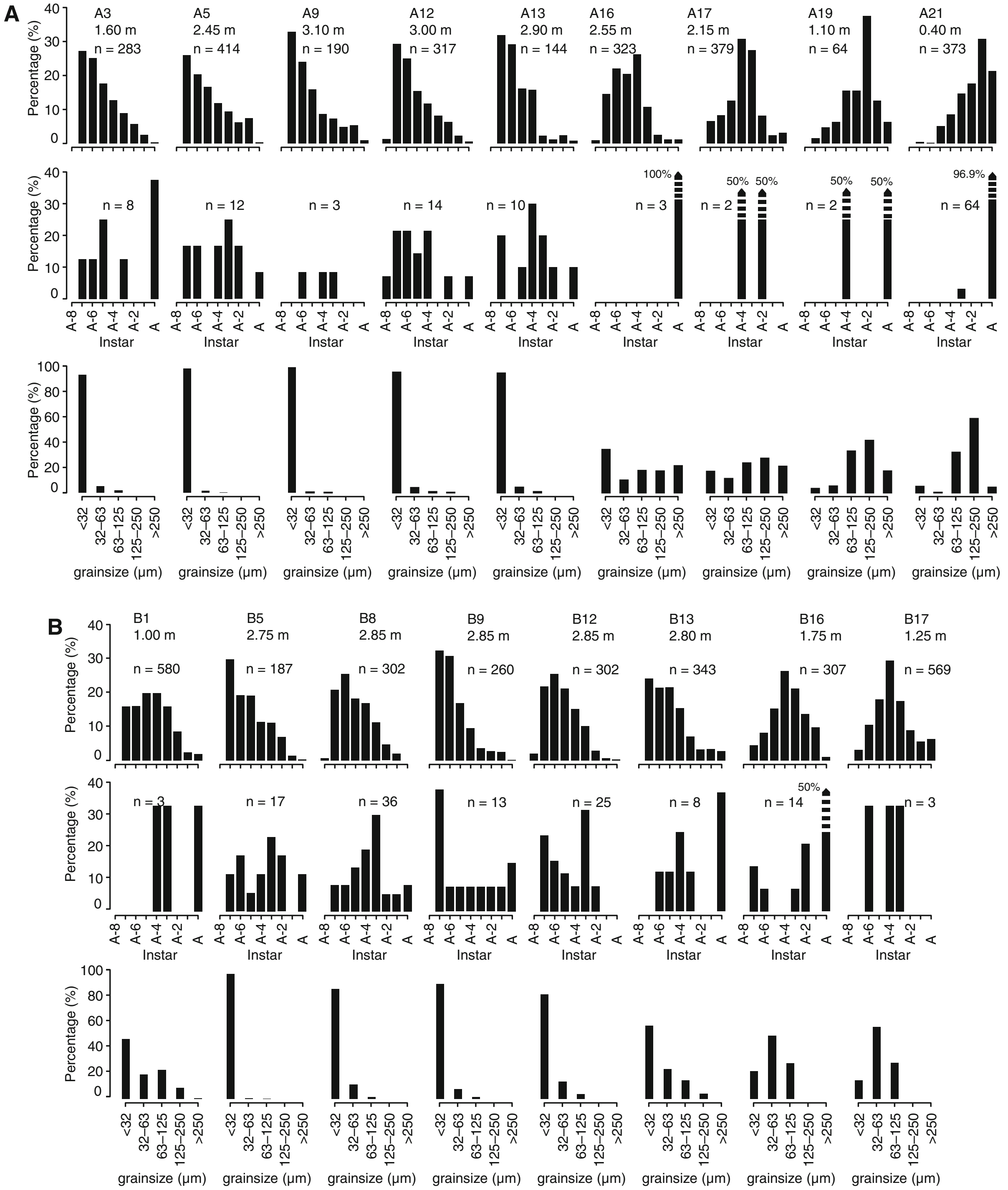
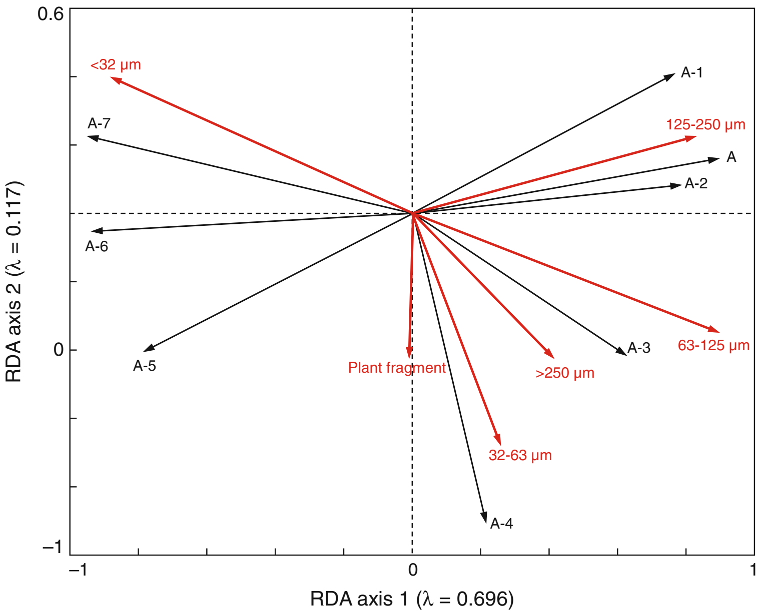


Fig. 6 Percentage histograms of different instars of subfossil (*upper row*), and living (*middle row*) populations of *L. inopinata* and the five grainsize fractions (*lower row*) in 17 surface-sediment samples from Hulun Lake. Sample number, water depth, and number of valves (for the subfossil populations) and carapaces (for the living populations) measured from a sample are shown in each histogram. **A** transect A, **B** transect B

Fig. 7 RDA biplot of percentages of different instars of subfossil *L. inopinata* and the environmental variables, including percentages of the five grainsize fractions and the plant-fragment abundance in 17 surface-sediment samples from Hulun Lake



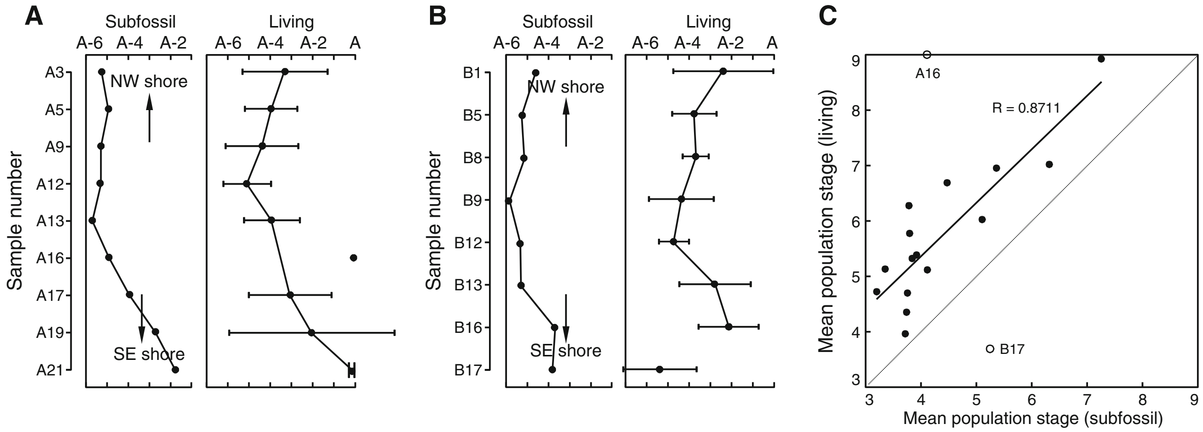


Fig. 8 **A** Within-lake changes in the mean population stage of the subfossil and living populations of *L. inopinata* along transect A. *Error bars* 95% confidence range for the estimation of mean population stage of the living population. **B** Same as A but for transect B. **C** Mean population stages of the living populations plotted against that of those subfossil populations in the 17 samples from both transects. R is Pearson coefficient calculated from 15 samples, with two outlier samples (hollow circles) excluded

The most probable pre-mortem process may be passive transport. *L. inopinata* is an epifaunal species that resides on the surface and in very shallow depths of the sediment (Decrouy et al., 2012). It is thus likely that the wave actions, surface currents, and other possible turbulences in the lacustrine environment could have caused suspending, drifting, and transport of the animals (and possibly eggs as well). The transported individuals would ultimately settle down at different energy regimes, resulting in a size-sorted pattern across the lake. This kind of transport would produce the identical result to post-mortem transport, except that the "transported" instars could further modify local population structures through subsequent developments and reproduction.

On the other hand, the excess of adults but scarcity of juveniles in the southeastern lake requires other explanations besides transport. As shown in Fig. 6, populations in the southeastern lake would not be sustainable unless enough earlier instars appear and molt to fill the gaps left by the death of the adults in a future time. One possibility is that in the forthcoming spring newly hatched juveniles would appear in this part of the lake (cf. Geiger et al., 1998) to continue the colonization. This would mean that the life cycle of *L. inopinata* varies greatly among different parts of the lake, with the littoral populations displaying significant seasonality, while the lake-center populations consist of overlapping generations (cf. Fig. 6). However, previous investigations (e.g., Geiger et al., 1998; Yin et al., 1999) suggested similar life cycles (except for the overwinter strategy) for *L. inopinata* residing in different lacustrine environments. Also, the fact that the mean stages of the living populations are by similar magnitudes more advanced than the mean stages of the subfossil populations from the same sites suggests that the contemporary living populations across the lake are situated at the same position on their annual cycles. This is contrary to the hypothesis that they have asynchronous life histories. Thus, we think active migrations may have occurred. Although early juveniles of *L. inopinata* may be washed away from shallow waters to greater depths, they may migrate back to the same areas as they grow larger. In this way, the shallow parts of the lake would be dominated by later instars albeit with fewer occurrences of earlier juveniles. However, the migration hypothesis needs information about how large a distance and by what means these small creatures are able to migrate during their life (cf. Table 1).

The accumulation of *L. inopinata* adults in the littoral zone (sample A21) of Hulun Lake is not unique. One of us has observed similar dense summer populations dominated by *L. inopinata* adults in the littoral zones of two small lakes in eastern Inner Mongolia (unpublished data). This probably implies that the adults of *L. inopinata* choose the littoral zone for laying eggs, to disperse the offspring across the lake through wave actions or via surface currents. Further investigations are needed to understand the significance of this behavior.

In addition to the hydrodynamic and possible migratory explanations of spatial variations in population structure, morphological features and intrinsic population dynamics may also contribute to population structure. The instars of different growth stages are quite different in body size and appendage structure, and thus may have different abilities to catch food, escape from predators and to tolerate changes in the environment. In this sense, differences in mortality rate could be expected for different instars, at different depths or in different seasons. Unfortunately, because of possible transport (either pre- and post-mortem) and migration, it is difficult to determine the actual rates of mortality and breeding from our subfossil data. And such information cannot be drawn from our seasonal data on living populations.

In summary, the spatial heterogeneity of the population structure of *L. inopinata* in the surface sediments of Hulun Lake may have resulted from both pre- and post-mortem processes including transport, migration, and intrinsic population dynamics. The relative contributions of these factors remain largely unknown, but our data suggest that the spatial contrast in population structure has begun to establish while the populations are still living.

It is not clear if the pre-mortem processes also play a role in the cases of marine ostracodes (Whatley, 1983, 1988; Ruiz et al., 2003), or in the cases of other lakes, as the hydrodynamic settings vary among these environments, and the species investigated differ. Nonetheless it is noticeable that at least the living populations of *Paradoxostoma variabile*, *Hirschmannia viridis*, and *Heterocythereis albomaculata* in the British coast show a size-sorted pattern of more late instars in the upper parts of the intertidal zone and more early instars in the lower parts, which was attributed to the spatial contrast in the ecological conditions across the intertidal zone (Horne, 1982). More studies focused on different species from different environments are needed to improve our understanding on the spatial difference in ostracode population structure.

Paleolimnological implications

The species composition and abundance of ostracodes as well as the population structure of the dominant species *L. inopinata* extracted from the surface sediments of Hulun Lake exhibit significant differences across the lakebed, demonstrating the potential of reconstructing the paleolimnological history based on the ostracodes from the sediment cores. As for species assemblage, a number of taxa including *Pseudocandona* sp., *Candona* sp., *C. mirabilis*, and *Plesiocypridopsis* spp. occur in the southeastern lake. There are, with fewer occurrences of these species in the northwestern lake, and they almost disappear in the central lake. Their abundances are closely correlated with plant fragment content in this study. These data suggest that the presence of the above taxa in sediment cores may be caused by an increase in the supply of terrestrial plant detritus, which in turn might denote the shrinkage of the lake and the approaching of the fluvial plains toward the core site, although it might also be due to changes in terrestrial vegetation or other catchment settings.

Judging from the age structure of *L. inopinata* (Fig. 6), the populations comprising more early instars, less middle instars, and few late instars occur in the central lake, implying that sediment cores containing such populations reflect periods of weak hydraulic energy and high lake level. The populations dominated by middle instars occur in the sub-littoral zone of the lake, denoting that these populations might be associated with the intermediate lake-level status. In the littoral zone of the lake, the *L. inopinata* populations consist mainly of middle and late instars with few early instars. These data imply that such populations might be linked with the condition of strong hydraulic energy and low lake level. In other words, increased early instars and decreased late instars in the *L. inopinata* populations in sediment cores could be indicative of the expansion of the lake and vice versa.

It is worth mentioning that the above inferences should be treated with caution. On one hand, the depth-related zonation of ostracodes is not a direct response of ostracodes to water depth itself (Holmes, 2001). Actually, it is the response of ostracodes to various factors such as the distribution of aquatic plants (Mischke et al., 2010), dissolved oxygen concentration (Martín-Rubio et al., 2005), organic detritus content (Jungwirth, 1979; this study), and temperature (Viehberg, 2006; Horne & Mezquita, 2008). Past shifts in the limnological condition could alter, to different extents, these factors and thus bringing uncertainties to the above interpretations. On the other hand, the spatial distribution of ostracode species and instars in Hulun Lake was based only on a low gradient of water depth albeit over a large gradient of offshore distance (Table 1). The low gradient of water depth would limit the availability of the inferred ostracode–depth relationship to large-scale expansions of the lake. Given that the lake level is much higher than present, the population structure of *L. inopinata* may turnover because the ecological condition could possibly serve as a major factor controlling the spatial distribution of the ostracodes instead of the hydrodynamic condition.

Conclusions

The subfossil ostracodes in the surface sediments of Hulun Lake are dominated by *L. inopinata* with frequently occurring *Ilyocypris* sp. and *Pseudocandona* sp., relatively rare *Candona* sp., *C. mirabilis*, and *Plesiocypridopsis* spp., and occasionally appearing *D. stevensoni* and *Notodromas* sp. Most ostracodes attain their maximum abundances in the southeastern part of the lake where plant fragments are rich in the substrate, indicating that terrestrial plant detritus would be the major factor controlling the species occurrence of ostracodes in the lake.

The population structure of subfossil *L. inopinata* exhibits significant spatial difference across the lake, with younger populations dominated by earlier instars in the central lake, while advanced populations are dominated by middle and later instars in shallower waters. Different instars are associated with different grainsize fractions of the substrate, indicating a hydraulic control on the distribution of instars. The within-lake change in the mean population stage of the living population at the time of sampling matches that of the subfossil population, suggesting that a spatial contrast has begun to form when the population is still living. The observed spatial heterogeneity of population structure of *L. inopinata* in Hulun Lake might mainly result from the hydraulic-driven pre- and post-mortem transport across the lake, but ecological factors such as migratory behavior, intrinsic population dynamics, and life cycle might also play a role. Further studies focused on the living population are needed for better understanding of the mechanism.

Spatial variations in the species occurrence of ostracodes and the age structure of *L. inopinata* in Hulun Lake provide valuable insights into paleolimnological reconstructions of the lake based on data of the ostracodes in the sediment cores. The relationship generated for the ostracodes and water depth in this study should be used with caution in terms of the limited gradient of present water depths.

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