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PRIMARY RESEARCH PAPER

Differential transport and preservation of the instars of *Limnocythere inopinata* (Crustacea, Ostracoda) in three large brackish lakes in northern China

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Abstract Population age structure, preservation, and carapace abundance of the valve remains of *Limnocythere inopinata* in 88 surface-sediment samples from Lakes Daihai, Dali, and Hulun were examined to better understand taphonomy of limnic ostracods. The spatial changes in population structure of *L. inopinata* match the within-lake hydraulic gradients, with the older instars preferentially deposited in the littoral zone while the younger instars being more abundant in deeper waters. We propose that molt and mortem remains of ostracods, especially those of the small juveniles, experience downslope transport. The magnitude of transport in a lake is controlled by wind-driven hydrodynamics. There is no chemical dissolution of ostracod valves in these alkaline lakes, and degradation is mainly represented by physical breakage. The preservation of *L. inopinata* is related to sedimentation rate and hydraulic stability, and the spatial pattern of preservation varies between lakes. Spatial and seasonal changes in sedimentation rate and hydraulic condition, and the ostracod life cycle may have contributed to this complexity. Adult and A-7 carapaces are the most frequent among the instars. We suggest that the preferential preservation of juvenile carapaces is either related to high mortality rate or to the good preservation in deep waters.

Keywords Ostracod · Population structure · Transport · Preservation · Taphonomy

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Introduction

Ostracods, micro-crustaceans whose calcareous valves can be preserved in the sediments, provide records of the past in their taxon composition and shell chemistry (Chivas et al., 1985; Xia et al., 1997; Li et al., 2012). Such signatures, indicative of past ecological conditions though they are, inevitably suffer from taphonomic modification, such as transport (Whatley, 1983; van Harten, 1986; Scharf et al., 1995; Meireles et al., 2014), physical and chemical degradations (Belmecheri et al., 2009; Blome et al., 2014), and temporal averaging (Park et al., 2003; Alin & Cohen, 2004). A reliable interpretation of fossil data requires a comprehensive understanding of the taphonomic processes.

The occurrence of transport may be identified from population age structure. Various studies have been undertaken on the population age structure of marine (Horne, 1982; Whatley, 1983; van Harten, 1986; Whatley, 1988; Błachowiak-Samołyk & Osowiecki, 2002; Ruiz et al., 2003; Błachowiak-Samołyk & Angel, 2007) and non-marine (Mezquita et al., 2000; van Doninck et al., 2003; Castillo-Escrivà et al., 2013) ostracods. Most of these studies have been focused on living faunas (Horne, 1982; Mezquita et al., 2000; Błachowiak-Samołyk & Osowiecki, 2002; van Doninck et al., 2003; Błachowiak-Samołyk & Angel, 2007; Castillo-Escrivà et al., 2013), and little attention has been paid to the valve remains and the taphonomic processes experienced in these communities. Whatley (1983, 1988) and Boomer et al. (2003) have presented diagnoses for thanatocoenosis (autochthonous) and taphocoenosis (allochthonous) valve assemblages, based on population age structure and other characters such as valve/carapace ratio, but these diagnoses need to be tested and refined with realistic data. Investigations of the spatial changes in population age structure of ostracods in sediment provide such data. Recently, Zhai et al. (2013) investigated the population age structure of *Limnocythere inopinata* (Baird) in a large, shallow lake in northern China. Their data revealed significant differences in population structure among different hydraulic regimes and shed light on the transport of ostracods in limnic systems. Since lakes (and marine habitats) differ from each other in their natural settings and hydrological processes, further comparative studies of different wetlands are important to better understand ostracod transport.

Selective degradation, on the other hand, may modify the ostracod assemblage structure (Danielopol et al., 1986; Park et al., 2003). It is not unusual for certain taxa to be absent from the assemblage due to low preservation potential (Danielopol et al., 1986). Under some circumstances there may be total dissolution of calcareous shells (Belmecheri et al., 2009). Despite both experimental (Kontrovitz, 1967) and field (Danielopol et al., 1986) investigations of the physical and chemical degradations of ostracod carapaces, the existing data are far from adequate to provide a comprehensive understanding on the differential preservation of ostracods. In particular, there has been little study of the differences between different species, different instars, or different lake systems.

In this paper, we investigate the population age structure of *L. inopinata* valve remains at multiple sites in Lakes Daihai and Dali in Inner Mongolia, northern China. Comparisons are made with the previously published results from Lake Hulun (Zhai et al., 2013) to obtain a more comprehensive understanding of ostracod transport. Moreover, the states of preservation of different instars of *L. inopinata* in the three lakes are studied. Efforts are made to describe the within-lake transport of different instars, as well as the differential preservation of instars under various environments. This study aims to improve our knowledge of the early taphonomic processes of limnic ostracods.

Materials and methods

Study sites

Lakes Daihai, Dali, and Hulun are located along the southeastern–eastern margin of the Mongolian Plateau (Fig. 1). They are among the major lakes of Inner Mongolia, and have been sites of much paleolimnological study in recent years (Xiao et al., 2004, 2008, 2009; Zhai et al., 2011). These lakes differ in size and shape (Fig. 1; Table 1). Lake Daihai is situated in a basin surrounded by mountains with peak of 2,305 m a.s.l. (a.s.l.: above sea level) that extends more than 1,000 m above the lake level (Wang & Wang, 1993). Both Lakes Hulun and Dali are bordered by low hills on their northwestern shores, and by flat plain on other sides. Sand dunes are distributed in the lacustrine plain to the east of Lake Hulun, as well as in the Hulandaga Desert Land to the south of Lake Dali. The lake-floor slopes of all lakes are mostly gentle due to the large sizes and relatively small depths of the lakes, although dip angles of nearly 6° are found in some parts of Lake Dali (Fig. 2).

The lakes lie near the northern margin of the East Asian Monsoon regime, where precipitation is limited while evaporation is intensive, resulting in brackish and alkaline water conditions (Table 1). Northwesterly winds prevail and produce frequent waves, especially in Lakes Dali and Hulun. Probably owing to the turbidity of the water, aquatic plants are scarce and are confined to river-mouth areas and a few sites in the littoral zones (Xu et al., 1989; Wang & Wang, 1993; Meng et al., 2007).

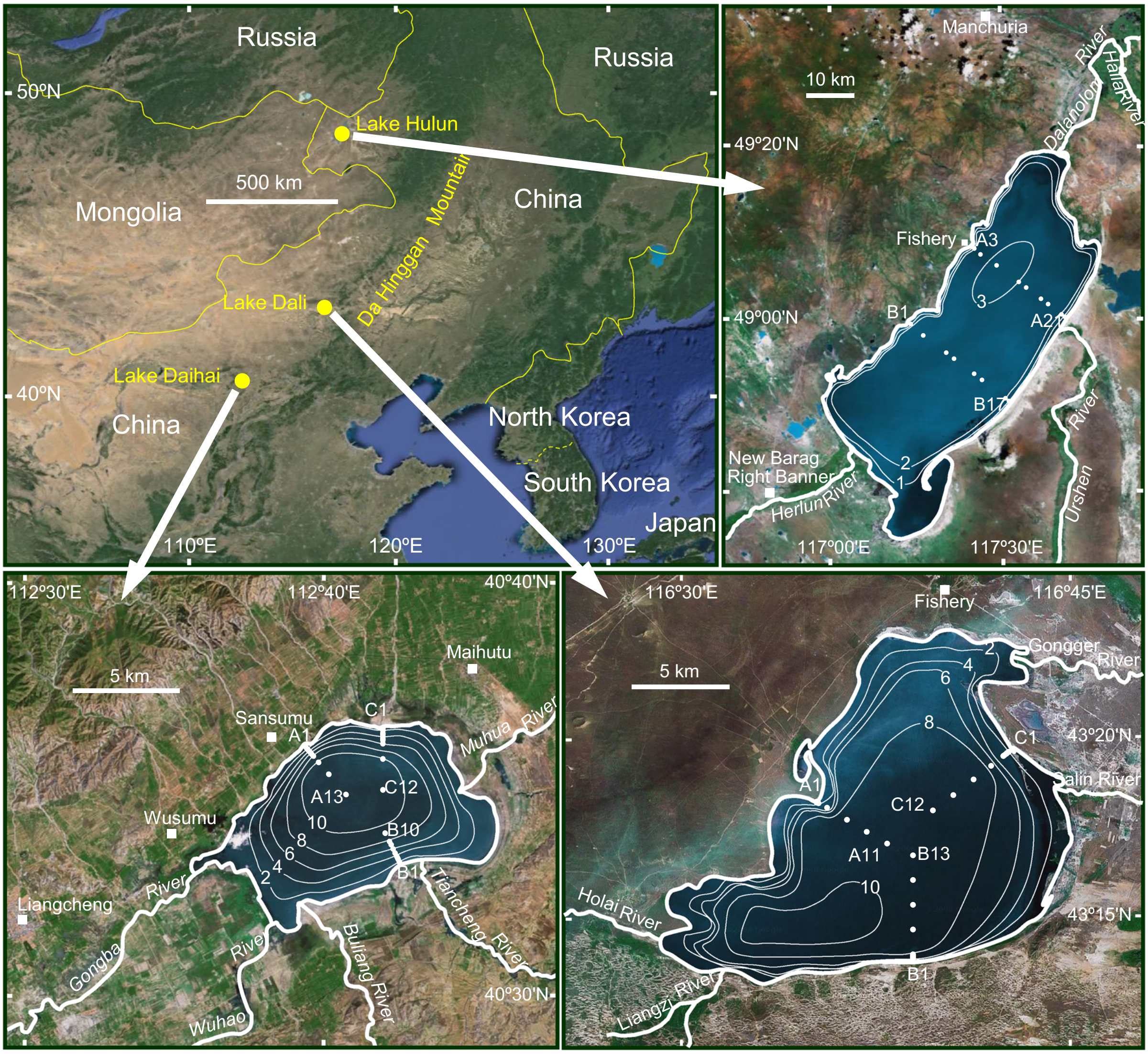


Fig. 1 Maps (from http://maps.google.com) showing the geographical locations of Lakes Daihai, Dali, and Hulun, as well as the sampling sites in the lakes. *White solid squares* indicate settlements (cities, villages, and fisheries). *Enclosed lines* with numerals represent bathymetry (*contour* in meters)

The modern natural vegetation in the study area is dominated by temperate steppe (Compilatory Commission of Vegetation of China, 1980). Alpine meadows and forests occur in the mountains surrounding Lake Daihai (Wang & Wang, 1993). Sparse, open woods, and shrubs colonize the Hulandaga Desert Land to the south of Lake Dali (Li, 1993), as well as the sand dunes to the east of Lake Hulun (Xu et al., 1989).

Human activities around the three lakes differ. The city of Liangcheng and a number of villages are built on the lacustrine plain to the west and north of Lake Daihai, where farmlands are cultivated (Fig. 1). There is a power station on the southern bank. By contrast, population density is low in areas around Lakes Dali and Hulun. There are no settlements around these two lakes except for a few fishing villages (Fig. 1). Like many other lakes in northern China, the fish resource in these lakes has been decreasing due to overfishing and lake retreat in the past decades (Daihai: Lan et al., 2001; Zhang et al., 2008; Dali: Han, 2007; Hulun: Zhang et al., 2011), and the situation is worst in Lake Daihai.

Table 1 Natural settings of Lakes Daihai, Dali, and Hulun

	Daihai	Dali	Hulun
Latitude (N)	40°29′–40°37′[a]	43°13′–43°23′[b]	48°31′–49°21′[c]
Longitude (E)	112°33′–112°46′[a]	116°29′–116°45′[b]	117°0′–117°42′[c]
Elevation (m a.s.l.)	1,216	1,224	540
Mean annual precipitation (mm)	413[d]	300–350[b]	247–319[c]
Mean annual evaporation (mm)	1,033[d]	1,287[b]	1,400–1,900[c]
Mean annual temperature (°C)	5.4[d]	1–2[b]	0.3[c]
Mean January temperature (°C)	−12.6[d]	−23 to −24[b]	−21.2[c]
Mean July temperature (°C)	20.7[d]	16–17[b]	20.3[c]
Annual mean wind speed (m s^{-1})	2.5[a]	2.8–3.0[b]	5.2[c]
Fresh-gale days per year	10[a]	35[b]	29 to >40[c]
Surface area (km^2)	80[e]	192[f]	1,774[g]
Catchment area (km^2)	2,313[e]	No data	37,214[c]
Maximum depth (m)	10.8	10.2	3.15
Salinity (g l^{-1})	4.7	7.6	2.5
pH	8.6	9.5	9.2
Freezing season	Nov–Mar[a]	Nov–Apr[b]	Nov–Apr[c]

Fresh gale means strong wind with flow velocity greater than 17 m s^{-1}. Unlabeled values were measured by the present authors in May 2010 (Daihai), June 2010 (Dali), and August 2009 (Hulun), respectively

[a] Wang & Wang (1993), [b] Li (1993), [c] Xu et al. (1989), [d] Zhou & Jiang (2009), [e] Wang et al. (2006) (measurements in 2002), [f] Liu & Li (2010) (measurements in May 2010), [g] Wang et al. (2012) (measured in 2011)

Methods

A gravity corer was used to sample the top 1 cm of sediments from a total of 88 sites in the three lakes (Figs. 1, 2). These include 35 sites in Lakes Daihai (site codes initiated with 'DH-,' visited in May 2010), 36 sites in Lake Dali (site codes initiated with 'DL-,' visited in June 2010), and 17 sites in Lake Hulun (site codes initiated with 'HL-,' visited in August 2009). These 1-cm samples may cover the past one to three decades as estimated from the age-depth models of the sediment cores retrieved from these lakes (Xiao et al., 2004, 2008, 2009). In the laboratory, ostracod valves were extracted from freeze-dried samples following the method described by Zhai et al. (2010, 2013), which used Na_2CO_3-buffered H_2O_2 solution (pH 9–10) to disaggregate the sample before it was sieved and then pipetted onto some glass plates for microscopic examination. No distinction was made between the valves of 'living' and 'dead' specimens.

Limnocythere inopinata is the dominant ostracod in the three lakes (Zhai et al., 2010, 2013). In Lakes Daihai and Dali, usually 50–100 randomly selected valves of *L. inopinata* from each sample were scored. In Lake Hulun, usually more than 150 randomly selected valves of *L. inopinata* were scored from each sample. Data on the population structure of *L. inopinata* in Lake Hulun have been published in Zhai et al. (2013), whereas data on the preservation of *L. inopinata* from this lake are presented here for the first time.

For the study of population structure, the development stages of juvenile *L. inopinata* were estimated from a valve length–frequency distribution. Adults were recognized by the radial pore canals on the free valve margin, because in adults the fused zone where the radial pore canals are situated is relatively broad while in juveniles it is very narrow, or invisible (Fig. 3; cf. Zhai et al., 2013). Lengths of broken juvenile valves were calculated from dimensions such as heights or the distances between anterior/posterior margin and the central muscle scars (cf. Zhai et al., 2013). Seriously damaged valves from which no measurements could be obtained were comparatively rare (<4%). It is noted that size–frequency distributions and length–secondary dimension relationships were investigated for each lake individually due to the slight inter-lake difference in the morphology of *L. inopinata*. Following international convention, growth stages were designated A, A-1, A-2, etc., with A being the adult and A-8 being the earliest instar. When necessary, the growth stages were divided into early (A-8–A-6), middle (A-5–A-3), and late (A-2–A) classes.

Mean population stage (MPS) of *L. inopinata* in each sample was calculated. This index was modified from Kock (1992) and Błachowiak-Samołyk & Osowiecki (2002) as follows:

$$\mathrm{MPS}=\frac{n_A\times 9+n_{A-1}\times 8+n_{A-2}\times 7+\cdots+n_{A-8}\times 1}{(n_A+n_{A-1}+n_{A-2}+\cdots+n_{A-8})}.$$

The MPS represents the mean development stage of the valve population. Larger MPSs indicate more advanced populations.

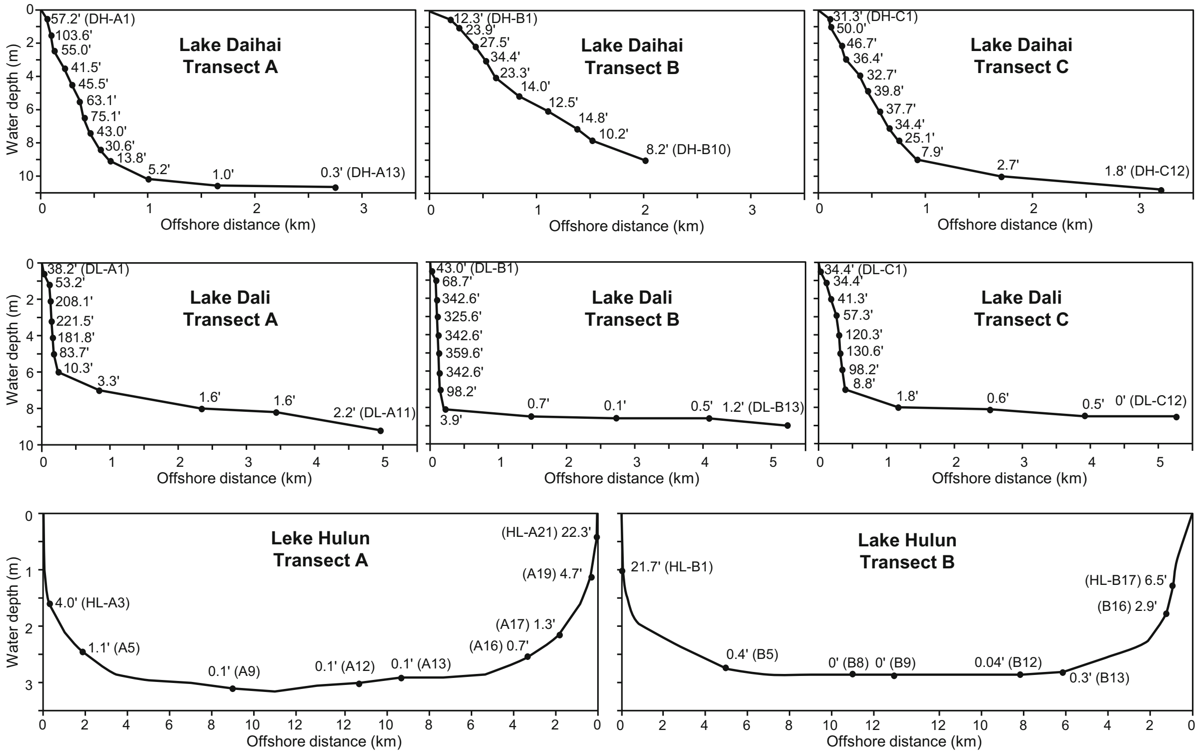


Fig. 2 Sampling sites in Lakes Daihai, Dali, and Hulun. Angles of inclination of the lake floor at the sites are calculated from the measured water depths and offshore distances, and are expressed in minute (1′ = 1°/60)

Preservation of valves was assessed using color, chemical overgrowth, dissolution, microbial colonization, as well as the degree of mechanical breakage. The valves were sorted into seven breakage grades (BD, Breakage Degree) depending on the area that has been lost due to mechanical damage, i.e., BD0 for intact valves, BD1 for those with 5% valve area broken away, BD2 with 5–10% area broken away, BD3 with 10–30% area broken away, BD4 with 30–50% area broken away, BD5 with 50–70% area broken away, and BD6 with over 70% area broken away. For inter-sample comparisons, the preservation of *L. inopinata* in a sample was measured by the percentage of intact valves (IV, %), i.e., BD0 valves. IV values in the early (E), middle (M), and late (L) age classes were calculated separately. Age classes with <10 valves found in a sample were discounted.

We used only specimens that retained the central muscle scars, which are situated in an elongated depression in the central part of the valve of *L. inopinata*. Fragments without central muscle scars were discarded in all the observations. Moreover, shells filled with aggregated sediment, those coated with chemical overgrowth, and those showing changes in color such as yellow and brown were discounted in the studies of population structure and mechanical breakage, because they may have been reworked from the old strata (Li et al., 2002). These shells were in small numbers (see "Results" section).

We also made notes about the carapaces (i.e., articulated valves) found in each sample. Each carapace was counted as two valves.

Results

Population age structure of *Limnocythere inopinata*

A total of 9,214 valves were measured for population age structure of *L. inopinata* in samples from Lakes Daihai (2,377 valves), Dali (1,764 valves), and Hulun (5,073 valves). The valves were identified as 9 development stages, including 8 juvenile stages and

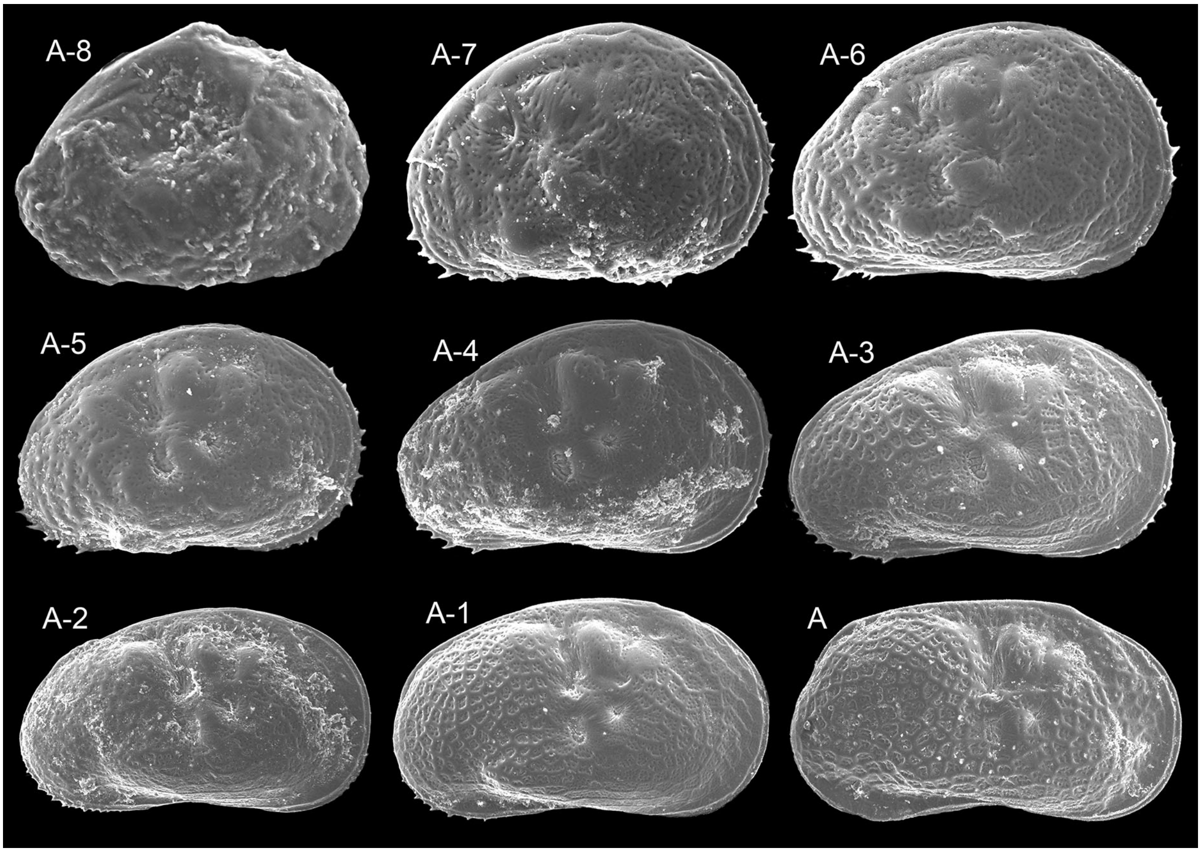


Fig. 3 *Limnocythere inopinata* belonging to different development stages. All are right valves from Lake Dali. Stage, specimen codes, and lengths are as follows. *A-8*, DL C10–60, 100 μm, deformed at the dorso-central part due to the softness of the shell of this stage; *A-7*, DL C10–37, 135 μm; *A-6*, DL C10–14, 160 μm; *A-5*, DL C10–52, 180 μm; *A-4*, DL C10–40, 240 μm; *A-3*, DL C8–35, 315 μm; *A-2*, DL C8–45, 340 μm; *A-1*, DL C8–43, 450 μm; *A*, DL C8–54, 495 μm. The photos were taken with an LEO 1450VP scanning electron microscope

the adult stage (Fig. 3). Very few A-8 valves were found among the instars, probably due to the low preservation potential of their poorly calcified, soft shells (Fig. 3; also see Zhai et al., 2013). Valves of the other stages were recovered abundantly. Thus, the populations discussed in the present paper mainly contain the stages A-7–A. As shown in Fig. 4, the population age structure of *L. inopinata* displays obvious within-lake difference, but the pattern and extent of spatial heterogeneity vary from lake to lake.

In Lake Daihai, valve remains of *L. inopinata* show only slight size sorting (Fig. 4). Populations in the littoral zone (sites DH-A1, B1, B2, and C1) are dominated by middle-age classes, with maximum instar frequency occurring between stages A-6 and A-2. In the deeper parts of the lake, instar dominance gradually shifts toward the early juveniles and such dominance becomes the most overwhelming in the depths of 6–9 m (DH-A8–A10, B7–B8, and C7–C9). In these samples, the A-7 juveniles show extraordinarily high frequency. In the deepest parts of the lake, early juveniles lessen, while middle and late instars recover (Fig. 4). MPS of *L. inopinata* ranges 3.2–6.5 and co-varies with instar composition (Fig. 5). It displays a decreasing trend from the littoral zone down to the depths of 6–9 m, and then slightly increases toward the lake center. The decrease of MPS in the shallower waters is more obvious in transect B than in the other two transects (Fig. 5).

In Lake Dali, spatial heterogeneity of the population structure of *L. inopinata* is characterized by the late-instar dominance in the shallow waters, the early-instar dominance in the profundal zone, and the transitional population structure in the intermediate

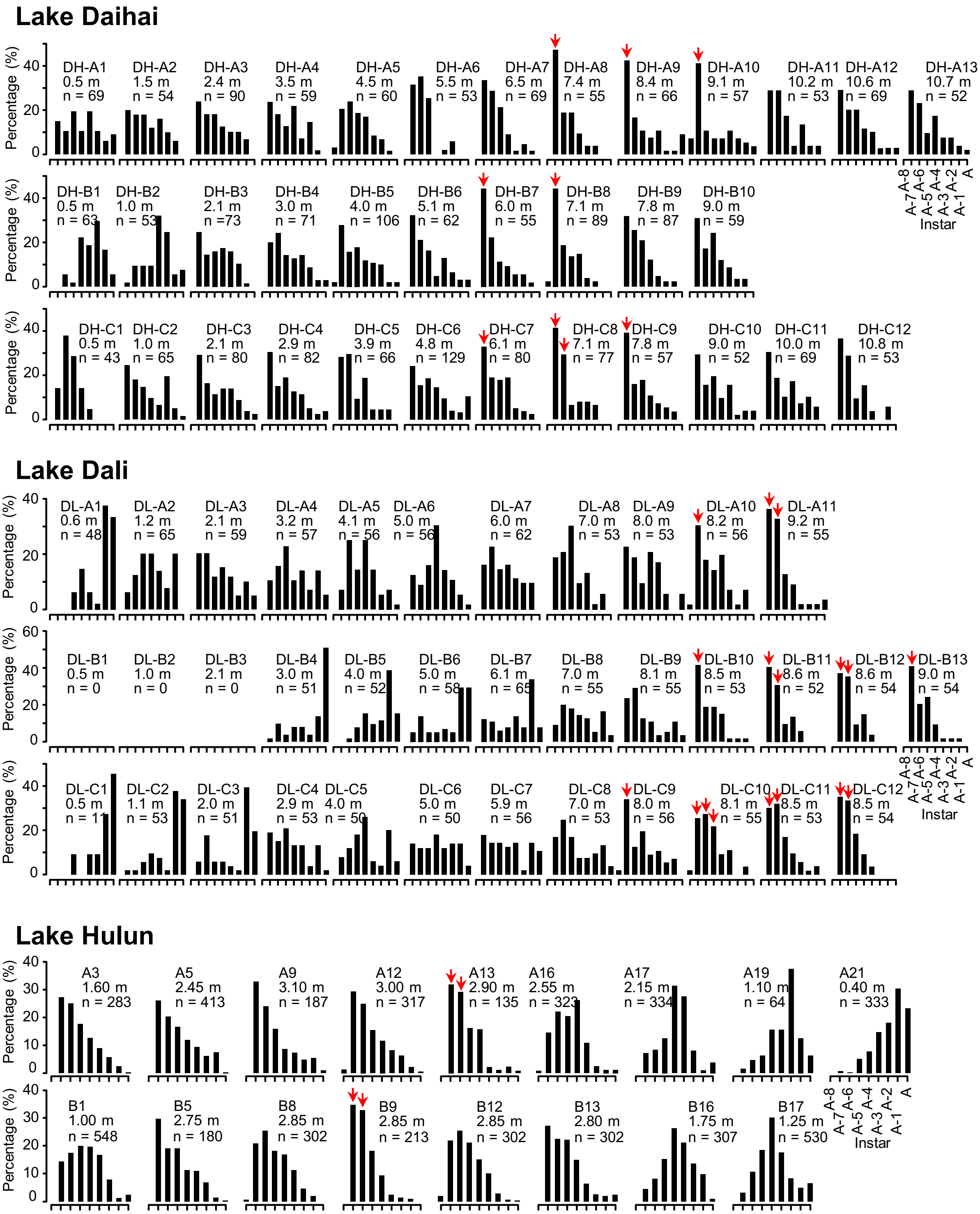


Fig. 4 Percentage histograms of different instars of *Limnocythere inopinata* in surface-sediment samples from the lakes. Sample codes and the number of valves measured in each sample are shown. Note that only a very small number of A-8 instars were found in the samples. *Red arrows* indicate high frequencies of early juveniles mentioned in the text. The panel of Lake Hulun is modified from Zhai et al. (2013)

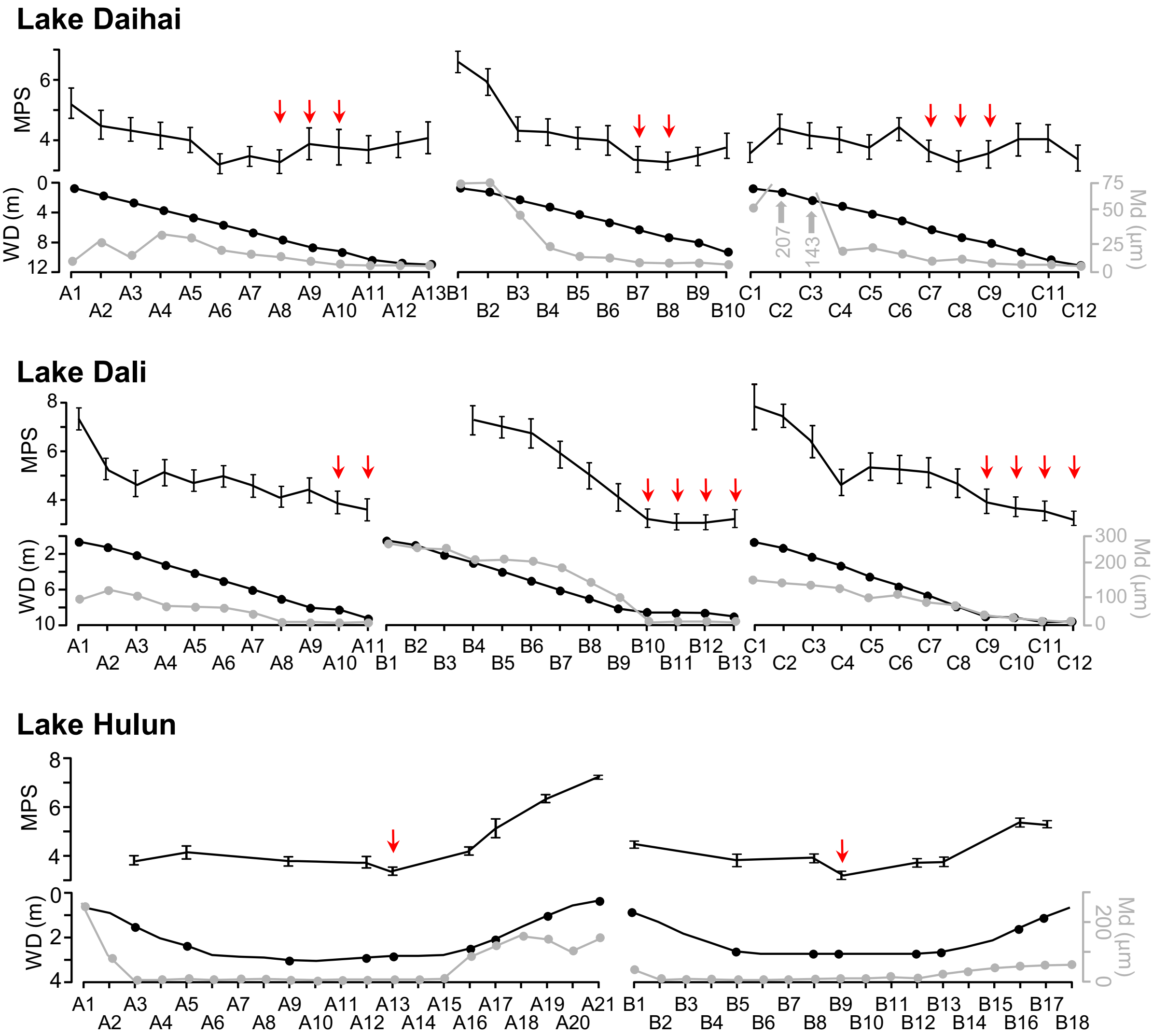


Fig. 5 Changes in mean population stage (MPS) of *Limnocythere inopinata* along the transects in the lakes. *Vertical error bars* represent 95% confidence ranges calculated with a Gaussian distribution model. Water depth and median diameter (Md) of the substrate at each site are shown. *Red arrows* indicate samples with high frequencies of early juveniles (see Fig. 4). Data of Lake Hulun are from Zhai et al. (2013)

depths (Fig. 4). In the shallow parts of the lake (sites DL-A1, B4–B7, and C1–C3), valve remains are dominated by the oldest instars A-1 and A. Frequency distribution of the other instars either forms a secondary peak around A-4 (samples DL-A1, B5, and C2), or displays irregular patterns. The lower limit of the late-instar-dominance zone in transect B, which is about 6.1 m (site DL-B7), is significantly deeper than those in transects A (around 1 m) and B (2–3 m). In samples from the intermediate depths (DL-A2–A9, B8–B9, and C4–C8), there is no clear pattern of instar dominance, although percentages peak at middle stages in samples DL-A2, A5, A6, and C5. The profundal samples (DL-A10–A11, B10–B13, and C9–C12) are dominated by early juveniles that significantly outnumber the older instars. MPS of *L. inopinata* in Lake Dali varies between 7.8 and 3.3. It shows a continuous decrease along the depth profiles, albeit with attenuated changes in the flat central parts of transects B and C (Fig. 5).

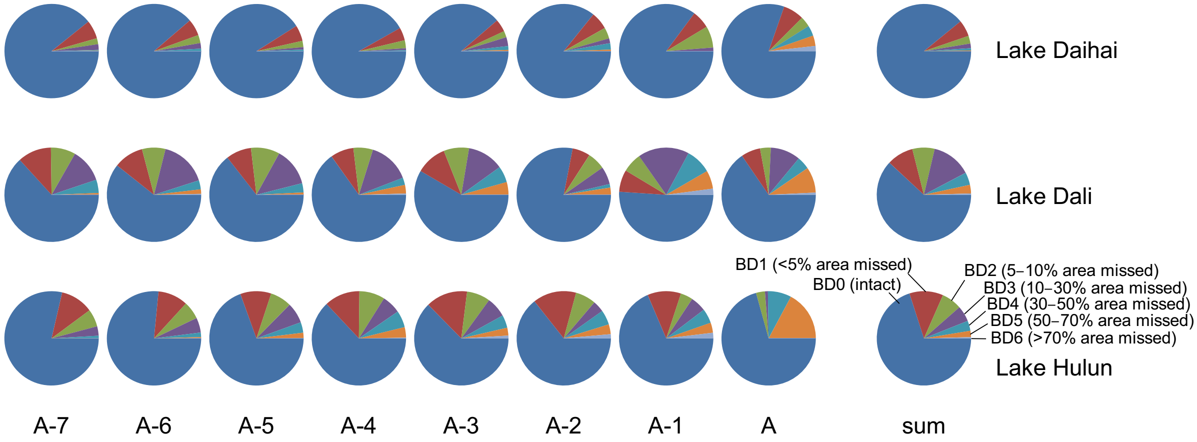


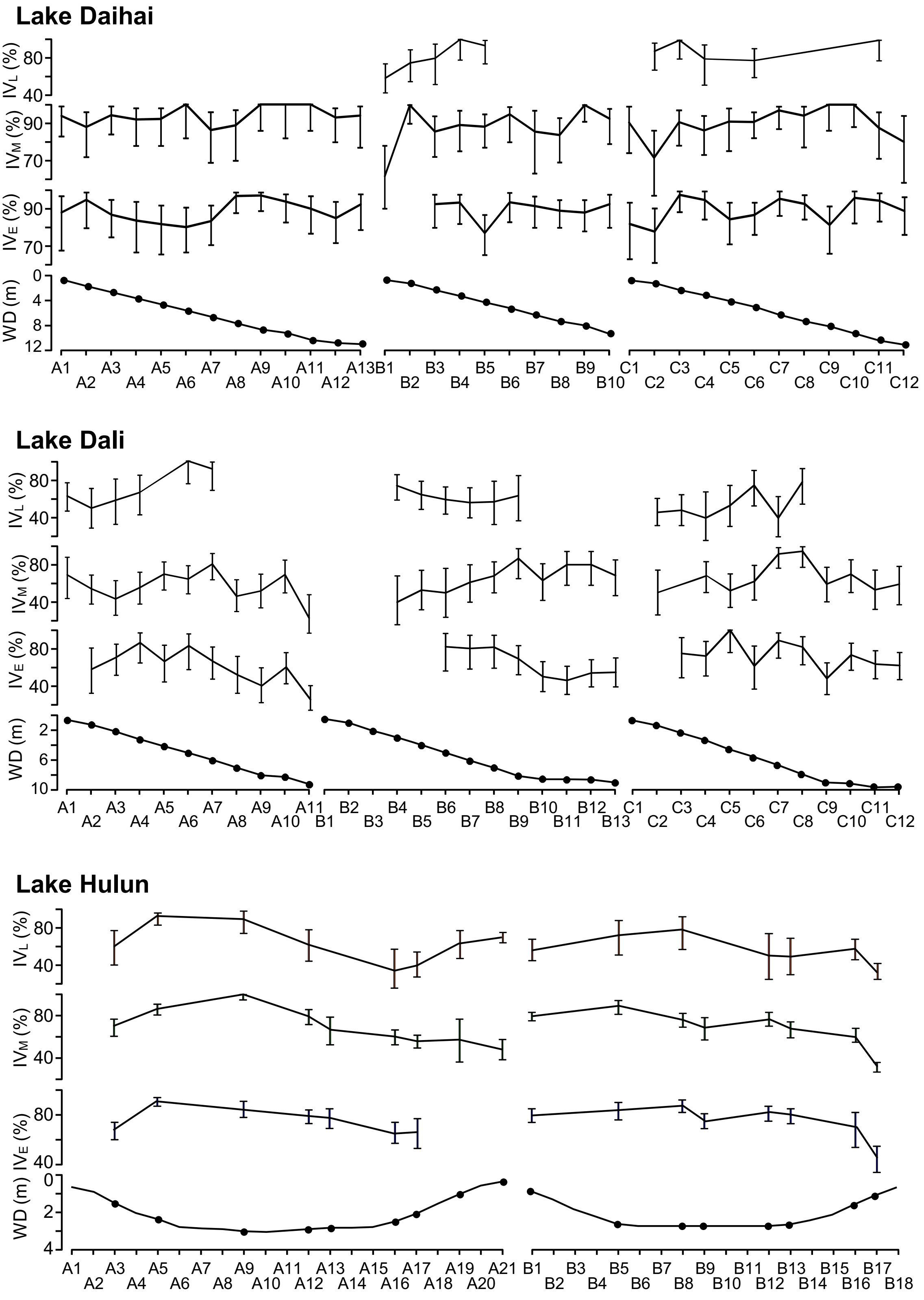
Fig. 6 Pie charts showing the preservation state of *Limnocythere inopinata* in the lakes. Percentages of valves belonging to different breakage degrees (BDs) are shown. *Each pie* is the combination of all the samples in a lake

The *L. inopinata* valves show typical size sorting across Lake Hulun (Fig. 4). Early-instar-dominated populations are present in the vast, flat central lake (sites HL-A9–A13, and B8–B13) as well as the northwestern sub-littoral zone (sites HL-A3, A5, and B5). At these sites, instar frequency peaks at stages A-7 and A-6, which lead a decreasing trend in the following stages. Middle-instar-dominated populations are found in the southeastern sub-littoral zone (samples HL-A16–A19, and B16–B17), as well as the northwestern littoral zone (sample HL-B1), where the populations display unimodal instar–frequency distributions. The late-instar-dominated population is found in sample HL-A21 in the southeastern littoral zone, with instar percentage peaking at the A-1 stage (Fig. 4). Since most of the changes in instar composition are present across the southeastern part of the lake, the most obvious changes in MPS also occur in this area (Fig. 5). MPS ranges, from the highest value of 7.3 in the southeastern littoral zone (site HL-A21), to the lowest value 3.2 in the central lake (site HL-B9). In the northwestern part of the lake, MPS shows only small changes (Fig. 5).

Preservation of valves of *Limnocythere inopinata*

The preservation states of 9,017 valves of *L. inopinata* were scored, comprising 2,372 valves from Lake Daihai, 1764 valves from Lake Dali, and 4,881 valves from Lake Hulun. In all samples, there is no evidence of chemical dissolution of valves. No specimen shows signs of decalcification, including softening, thinning, or pitting on the surface, as we observed in some samples deposited in low-salinity condition (Zhai et al., 2011) and in dissolution experiments (unpublished observation). There is little trace of microbial colonization on the valve surface, such as that described by Danielopol et al. (1986). In addition, only 0.1% of the *L. inopinata* valves in Lake Daihai and only 0.2% of those in Lake Hulun show changes in color (yellow and black, respectively). In Lake Dali, this percentage is 9.5%, but most of the colored shells (light to intermediate yellow, brown, black, or dirty white) are found in the littoral zone. About 6.6% of the *L. inopinata* valves in Lake Dali are filled with slightly or moderately aggregated substrate, and all of these are colored and are found in the littoral zone. Overall chemical and sedimentological alternations occur in only a small number of valves and are mainly confined to the littoral parts of the lake.

By contrast, physical degradation is evident in all of the samples and we focus here on mechanical breakage, in which part of the valve area breaks off and forms a gap in, usually, the valve outline. The extent of mechanical breakage of *L. inopinata* valves varies among different instars and among lakes (Fig. 6). In general, specimens from Lake Daihai are the best preserved among the three lakes, with 89.1% of the valves being intact (BD0, Fig. 6). Another 5.6% of the valves are only slightly damaged (BD1). Only 5.3% show higher breakage grades (BD2–6). Among the instars, the A-7–A-4 juveniles have similar states of


Lake Daihai
IVL (%)
80
40
IVM (%)
90
70
IVE (%)
90
70
WD (m)
0
4
8
12
A1 A2 A3 A4 A5 A6 A7 A8 A9 A10 A11 A12 A13
B1 B2 B3 B4 B5 B6 B7 B8 B9 B10
C1 C2 C3 C4 C5 C6 C7 C8 C9 C10 C11 C12
Lake Dali
IVL (%)
80
40
IVM (%)
80
40
IVE (%)
80
40
WD (m)
2
6
10
A1 A2 A3 A4 A5 A6 A7 A8 A9 A10 A11
B1 B2 B3 B4 B5 B6 B7 B8 B9 B10 B11 B12 B13
C1 C2 C3 C4 C5 C6 C7 C8 C9 C10 C11 C12
Lake Hulun
IVL (%)
80
40
IVM (%)
80
40
IVE (%)
80
40
WD (m)
0
2
4
A1 A2 A3 A4 A5 A6 A7 A8 A9 A10 A11 A12 A13 A14 A15 A16 A17 A18 A19 A20 A21
B1 B2 B3 B4 B5 B6 B7 B8 B9 B10 B11 B12 B13 B14 B15 B16 B17 B18

◀**Fig. 7** Spatial changes of the preservation of *Limnocythere inopinata* in the lakes. Percentages of intact valves (IV, %) in the early (*E* A-8–A-6), middle (*M* A-5–A-3), and late (*L* A-2–A) age classes are calculated. Results containing <10 valves are discounted. *Vertical error bars* indicate 95% confidence ranges calculated with a Chi-square distribution model

preservation, with 88.7–91.9% of the valves being intact. In stages A-4–A, the percentage of intact valves decreases gradually with age, reaching a level of 80.4% in the adult.

The *L. inopinata* valves from Lake Dali show the poorest preservation, with only 61.9% of the valves being intact (Fig. 6). Another 9.1, 7.7, and 13.6% are labeled BD1, BD2, and BD3, respectively. Only 7.7% are seriously damaged (BD4–6). Among the instars, the A-2 is the best preserved, with 78.0% of them being intact (BD0). Only 51.0% of A-1 are intact, being the worst preserved. The A-1 juvenile and the adult have the highest percentages (6.3 and 8.8%, respectively) of seriously broken valves belonging to BD5 (Fig. 6).

In Lake Hulun, the state of preservation is somewhat better than that of Lake Dali (Fig. 6). Of all the valves, 70.0% are intact (BD0). Another 11.6% belong to BD1, followed by 6.9% as BD2. A total of 5.4% of the valves are at BD3, and the rest 6.0% belong to BD4–6. Among the instars, the percentage of BD0 valves varies from 78.6% of A-7, which has the best preservation, to 62.6% of A-3, which has the poorest preservation. The adults contain a relatively great portion (17.1%) of BD5 valves.

The within-lake variations in the preservation state of *L. inopinata* valves are illustrated in Fig. 7. Specimens in Lake Daihai are generally well preserved, and the spatial differences in IV_E (intact early juvenile percentage) and IV_M (intact middle juvenile percentage) are small (Fig. 7). IV_L (intact late instar percentage) in most of the sites are discounted due to low specimen numbers, so it is difficult to known its spatial variation.

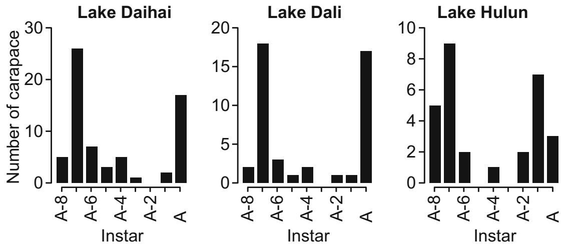


Fig. 8 Growth stage–frequency distribution of the carapaces of *Limnocythere inopinata* recovered from the lakes. All the carapace specimens from each lake are combined

In Lake Dali, changes in IV values of different age classes are not consistent (Fig. 7). IV_E shows a slight trend of decline in deeper waters. IV_M also declines in the deeper part of transect A, but rises in the deeper part of transect B and in the intermediate part of transect C (Fig. 7). It is difficult to know the preservation states of late instars in the central part of Lake Dali because of low specimen numbers.

In Lake Hulun, IV values of the three age classes show similar spatial changes (Fig. 7). IV values in the northwest-central lake (sites HL-A5, A9, B5, and B9) are the highest, with more than 80% of the specimens being intact. All the age classes show more serious damage toward the littoral zone, despite an obvious reversal of IV_L in samples HL-A19 and A21 (Fig. 7). The poorest preservations of all age classes are found in sample HL-B17.

Recovery of the carapaces of *Limnocythere inopinata*

A limited number of carapaces (i.e., articulated bivalves) have been recovered, including 66 from Lake Daihai, 45 from Lake Dali, and 29 from Lake Hulun (Fig. 8). Due to the small number, it is difficult to assess the within-lake distribution of carapaces. Instead, all the specimens from the same lake are combined together to study the preservation potential of the carapaces of different growth stages.

Carapaces of the early and the late growth stages are significantly more frequent in all lakes than those of the middle stages (Fig. 8). In both Lakes Daihai and Dali, A-7 and A carapaces significantly outnumber the other instars. In Lake Hulun, considerable numbers of A-8, A-7, A-1, and A carapaces are found. Five of the seven A-1 carapaces in Lake Hulun are from sample HL-A21. Considering the scarcity of A-8 shells found in the samples (Fig. 4), the numbers of their carapaces are unexpectedly large. In fact, almost all the A-8 valves are found as carapaces.

Discussion

Causes for the within-lake difference of the population structure of *Limnocythere inopinata*

The population structure of the valve remains of *Limnocythere inopinata* displays significant within-lake differences in Lakes Daihai, Dali, and Hulun (Figs. 4, 5). In general, this pattern is characterized by more advanced populations in shallower waters and younger populations in deeper waters. The most striking feature requiring explanation is the outnumbering of earlier instars by later instars in shallow waters. Ostracods in the sediment are the total accumulation of all the instars occurring in various seasons of the past years (Park et al., 2003; Mischke et al., 2010). When living, each juvenile has a carapace that is shed in the process of molting, until adulthood is attained, when the animal no longer molts (van Harten, 1986; Meisch, 2000). Both the shed valves and the valves of the dead individual can be preserved in the sediment. Therefore each adult can potentially leave eight pairs of juvenile (A-8–A-1) valves and one pair of adult (A) valves. Since not all individuals could reach adulthood, the valve population should display a decrease along the molt sequence (van Harten, 1986). Consequently, any valve population with the younger instars outnumbered by the older instars cannot be 'virgin' (phrase adopted from van Harten, 1986), and the following possibilities should be considered: (1) selective preservation, (2) inter-habitat migration, and (3) valve-remains transport.

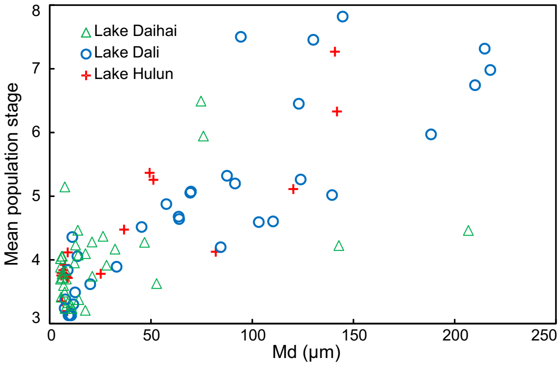


Fig. 9 Mean population stage of *Limnocythere inopinata* in the surface sediments plotted against median diameter (Md) of the samples

It is noted that here the phrase 'valve-remains transport' is proposed instead of 'post-mortem transport' used by Whatley (1983, 1988). This is because the valves found may include not only valves of dead individuals, but also those shed during molting. For the same reason, we use phrases such as 'valve remains' and 'valve deposits' instead of 'thanatocoenosis' ('thanatos' has the meaning 'death' in Greek).

The contribution of selective preservation, if any, should be minor in the present study. As shown above, there is no evidence that early juveniles are preferentially degraded in the shallow waters (Fig. 7), which could lead to their under-representation (Fig. 4). In fact, the low numbers of seriously broken valves (BDs > 4) in the samples do not seem to have significantly affected our estimation of the valve frequency of any instar between A-7 and A (Fig. 6).

Inter-habitat migrations, both active and passive, certainly exist due to the locomotion capability and the small size of ostracods. It is possible for currents and waves to carry living juveniles from the shallow waters to the deep waters. However, no matter how many early juveniles are taken away, the number of late instars emerging at a site should be always smaller than the number of the early juveniles living at the site, rather than being greater as observed in our littoral samples (Fig. 4). Although the upslope migration of late instars from the greater depths may explain such a pattern, the slow crawling of *L. inopinata* nearly excludes such possibility. We measured speeds <0.5 mm s^{-1} for the adult and much slower values for juveniles on clastic substrate in the petri dish. Considering the short life cycle of *L. inopinata* (about 1–1.5 month; Yin et al., 1999; Li & Jin, 2013; Xiangzhong Li, personal communication) and the large sizes of the lakes (Fig. 1; Table 1), it seems impossible for individuals of *L. inopinata* to migrate from the lake center to the littoral zone during their lives.

This leaves valve-remains transport to be considered as the mechanism leading to the observed abnormal population structure in the shallow parts of the lakes, where valves of earlier juveniles are outnumbered by those of later instars (Fig. 4). Here we partly adopt the explanation of Whatley (1983, 1988), which was originally proposed for marine ostracods. We suggest that in littoral environments where wave activity is intensive, valves of the younger juveniles are washed away after molting and also after the juveniles' death, leaving only shells of adults and late juveniles. Correspondingly, in deeper parts of the lake, with the decreasing disturbance in the bottom water, the transported valves settle down, resulting in deposits rich in early juveniles but poor in late instars. This explains both the dominance of late instars in the shallow waters and the excess of early juveniles in the deep waters (Fig. 4). The significant correlation between the mean population stage (MPS) of *L. inopinata* and the grainsize of the sediment (the latter is a proxy of hydraulic disturbance, see, e.g., Xiao et al., 2012, 2013) in the three lakes lends strong support to this explanation (Fig. 9). It indicates that instar valves of different sizes and weights are sorted to a certain extent and are preferentially deposited in different hydraulic regimes. Apparently, such transport depends on the natural settings of the lake and thus is lake-dependent, as we will discuss in details in the next section.

It is noted that although we consider valve-remains transport as the primary cause for the observed pattern, other factors such as temperature, dissolved oxygen, and life history may have also contributed to the within-lake heterogeneity of the population structure of *L. inopinata*.

Transport of *Limnocythere inopinata* in lakes

Lakes Daihai, Dali, and Hulun differ from each other in natural settings including size, shape, regional geomorphology, and climate (Fig. 1; Table 1). These factors are responsible for the hydrodynamics of the lake water. As a result, magnitude and pattern of ostracod transport vary among these lakes.

Lake Daihai has the weakest transport among the three lakes, with the smallest difference in the mean population stage (MPS) (Figs. 4, 5). In samples closest to the shore, only the early juveniles are washed away (Fig. 4). In Lakes Dali and Hulun, by contrast, the spatial difference of MPS is larger, and both the early and the middle juveniles can be removed from the littoral zone (Figs. 4, 5).

We propose that the different magnitudes of transport are mainly due to the different hydraulic levels of the lakes. As shown in Fig. 9, the overall substrate grainsize in Lake Daihai is the smallest among the three lakes, with Md at most littoral sites being smaller than 75 μm. Fine substrate texture is indicative of weak hydraulic disturbance (Xiao et al., 2012, 2013), which should have caused weak transport of ostracods. The weak hydraulic disturbance in Lake Daihai is in agreement with the less strong and less frequent wind action in the lake area (Table 1). This is in turn related to the presence of high mountains around the lake, which significantly attenuate the northwesterly winds. By contrast, Lakes Dali and Hulun are situated on unsheltered landscapes and thus wind action is much stronger (Fig. 1; Table 1), resulting in significant transport of ostracods (Figs. 4, 5).

Even within a lake, transport can differ. In Lake Daihai, ostracod size sorting is more obvious in the littoral parts of transect B (Figs. 4, 5). This may be related to the proximity of the mouth of River Tiancheng (Fig. 1), which has intensified the hydraulic mobility. In Lake Dali, transport is the most significant in transect B with the steepest slope (Fig. 2). In Lake Hulun, the majority of the hydraulic gradient, as well as the majority of ostracod transport occurs across the southeastern part of the lake (Figs. 4, 5). To the northwest of the lake, rocky hills serve as an obstacle to the prevailing northwesterly wind (Fig. 1) and wave action is less strong, as indicated by less prominent Md gradient (Fig. 5).

With respect to the pattern of transport, we propose that there is a limit below which transport ceases or greatly weakens, and that the position of this limit varies from lake to lake (Figs. 4, 5). For example, in Lake Daihai, with the increase of water depth, the frequencies of early juveniles in the population gradually increase until the sites DH-A8–A10, B7–B8, and C7–C9 (water depths 6–9 m), where the A-7 juveniles reach extraordinary excess and MPS decreases to the lowest levels (3.2–3.8) in the lake (Figs. 4, 5). This suggests that the transported A-7 juveniles are preferentially deposited in these sites, resulting in significant contamination of the local valve deposits. Consequently, below this limit, contamination by A-7 greatly diminishes.

In Lake Dali, preferential deposition of the early juveniles occurs at greater depths than in Lake Daihai due to stronger transport (Figs. 4, 5). It is in the deepest parts of the transects (sites DL-A10–A11, B10–B13, and C9–C12, water depths >8 m) that the abnormally high A-7 and A-6 percentages and the lowest MPS values (3.1–3.9) are observed (Fig. 4), indicating that the downslope transport does not cease in the deepest parts of the transects. We did not sample the deepest part of Lake Dali (ca. 10 m depth, in the southwest of the lake), but an earlier investigation (Zhai et al., 2010) revealed that this area contain sparse populations of *L. inopinata* that are very rich in early juveniles and are deprived of adults. So it is likely that downslope contamination has influenced the whole profundal area of Lake Dali.

In Lake Hulun, as discussed above, the transport is mainly from the southeastern littoral zone toward the central lake. As shown in Figs. 4 and 5, the enrichment of different instars occurs at different depths on the southeastern slope, and the excess of A-7 and A-6 instars occurs at the sites HL-A13 and B9. It is also at these two sites that MPS reaches the lowest values (3.4 and 3.2, respectively). To the northwest of this limit, MPS shows little change, and transport seems to be minor. Nonetheless, at least the site HL-B5 has been contaminated by A-7 juveniles transported from the shallower areas (Fig. 4).

Details such as when and how the transport of *L. inopinata* occurs are still unknown. Analysis of *L. inopinata* specimens with well-preserved soft parts from Lake Hulun (Zhai et al., 2013) revealed abundant early juveniles in the central lake while adults were abundant in the littoral zone, a pattern matching the population structure of the valve deposits. Since specimens recovered from ethanol-preserved samples may contain both living and recently dead individuals, the finding of Zhai et al. (2013) implies either passive migration or post-mortem transport, or both. But since passive migration of early juveniles, which would require the backward migration of late instars for balance, is improbable because of the slow movement of *L. inopinata* (see above), the observation of Zhai et al. (2013) may better be explained by the transport of recently dead early juveniles. More data (e.g., larger sample size, longer season span) are needed to confirm this. It is not known whether valves shed during molting are transported in the same way as the whole individual. The molted valves of ostracods are usually disarticulated (e.g., Danielopol et al., 1986; Whatley, 1988). Kontrovitz (1975) illustrated by flume experiments that single valves are more difficult to move than carapaces are, implying that the transport of shed valves may differ from that of the dead individuals.

Although the ostracods may be transported in various ways including floating, suspension, and saltation, direct observations on these processes are rare. Li & Jin (2013) collected abundant *Limnocythere inopinata* from a sediment trap placed at 10 m below the water surface at a site with water depth of 25 m in the central part of Lake Qinghai, the largest lake of China. A number of other researchers also observed the floating of ostracod shells (e.g., Eugen Karl Kempf, personal communication; Szlauer-Łukaszewska & Radziejewska, 2013).

Transport of ostracods may vary according to season. Changes in wind, water temperature, as well as ice cover could alter lake-water hydrodynamics. The three lakes studied are covered by thick ice during the winter (Table 1), when the disturbance of the bottom water nearly ceases. Thus the winter generations of ostracods may not be subjected to the same extent of transport before being buried by, for example, the mass deposition brought about by the dust storms that prevail in the spring.

State of preservation of valves

In this study, the preservation of *L. inopinata* is investigated mainly for physical breakage. Although pretreatment could have also caused damage, we considered this as being minor. Our pretreatment procedure is uniform for all the samples. And when the reaction with the H_2O_2–Na_2CO_3 solution is monitored, the similar intensities (bubbling, micro-currents, etc.) are observed except for a few sandy samples with weak reaction. The good recovery of many of the samples (e.g., $IV_{mean} = 89.1\%$ for Daihai samples, and in particular >98% for DH-A9 and A10) suggests that valve damage caused by pretreatment is insignificant. We believe that the observed valve preservation generally reflects the natural condition.

When the lakes are compared, Lake Daihai has the best preservation, both with respect to the intact valve percentage (IV), and the percentages of valves at specific breakage grades (Fig. 6). We suggest that the good preservation of *L. inopinata* in Lake Daihai may have benefited from the high sedimentation rate, weak hydraulic disturbance, as well as less intensive bioturbation.

Ostracods in environments with higher sedimentation rates are buried and isolated from various kinds of degradation more quickly (Danielopol et al., 1986). The sedimentation rates of Lakes Daihai, Dali, and Hulun are 1.2, 0.5, and 0.3 mm $year^{-1}$, respectively (Xiao et al., 2004, 2008, 2009). Although sedimentation rate may vary within a lake (e.g., Scharf et al., 2010), estimates based on cores from the deepest part of each lake are likely to reflect inter-lake differences. Thus the high sedimentation rate in Lake Daihai may have contributed to the good preservation of *L. inopinata*.

It is possible that agitation of sediment also damages ostracod valves (Kontrovitz, 1967). The hydraulic disturbance in Lake Daihai is weaker than Lakes Dali and Hulun due to gentler wind action (Table 1; also as mentioned above), which may also explain good preservation in Lake Daihai.

Predation and other kinds of bioturbation in the surface sediment are another possible cause of damage to ostracod valves. Ostracods are eaten by various kinds of animals such as fishes (Karanovic, 2012), dragonfly larvae (Schmit et al., 2012), and backswimmeres (Vandekerkhove et al., 2012). We do not have data on the biomass of meiobenthos in the three lakes, but the fish resource in Lake Daihai experienced the most severe reduction during the past few decades among the lakes.

Within the three lakes, there is no consistent spatial pattern of preservation change (Fig. 7). It is only in Lake Hulun that we observe a coherent pattern of change in the preservation of instars, which become more poorly preserved in the southeastern littoral zone. It may be inferred that the significant degradation in the littoral parts of Lake Hulun comes from strong disturbance. However, this explanation cannot be applied to Lakes Dali and Daihai (Fig. 7). Within-lake preservation differences in Lake Daihai are minor for all age classes. In Lake Dali, the early juveniles seem to be better preserved in shallow waters. Similarly, in the Tibetan lake Nam Co, ostracods are better preserved in the shallow and the intermediate waters than in the profundal zone (Zhu et al., 2010). Probably factors such as sedimentation rate and bioturbation have intervened to cause the above inconsistence.

When the preservation states of different instars are compared (Fig. 6), we see that both Lakes Daihai and Hulun have younger instars (A-7–A4 in Daihai and A-7–A-6 in Hulun) better preserved than older instars. In Lake Dali, by contrast, the A-2 instar shows the best preservation (Fig. 6). The mechanisms responsible for this are unknown and may be complex, considering that different instars would emerge at different times of the year and that the factors affecting preservation, such as hydraulic and biological perturbations, and sedimentation are likely to vary with season and with lake. Nonetheless, the better preservation of smaller, thin-shelled instars in Lakes Daihai and Hulun contradicts the experimental result of Kontrovitz (1967) that ‘stronger’ shells are more resistant to physical degradation. Unknown difference in the process of degradation in natural and laboratory environments may be involved.

It is also found that a significant portion of A and A-1 valves in Lakes Hulun and Dali are seriously damaged. The possibility that this has arisen from the higher fish densities in these two lakes cannot be ruled out but more information, including perhaps predation experiments, are needed to better answer this question.

It is reminded that transport cannot be directly linked to degradation. At least for Lakes Daihai and Hulun, the early juveniles do not show worse preservation in deeper waters, where they are supposed to have experienced long-distance transport (Fig. 7). In contrast, the late instars that are less likely to be transported show spatial preservation changes (Fig. 7).

Interpretation of carapace preservation

The low number of articulated valves (carapaces) recovered from the samples may be due partly to sample preparation. Yet the striking similarity between the instar carapace–frequency distributions of different lakes requires explanation other than pretreatment (Fig. 8). In all of the three lakes, carapaces of A-7 and A are comparatively frequent. The high frequency of adult carapaces is expected. Molting usually causes disarticulation (Danielopol et al., 1986; Whatley, 1988). Adult ostracods do not molt (van Harten, 1986; Meisch, 2000). Thus they have greater potential to be preserved as carapaces. However, juvenile carapaces can be preserved only in the case of infant mortality. The presence of a large number of juvenile carapaces, which is indicative of catastrophic infant mortality, is called the ‘Whatley effect’ (Danielopol et al., 1986). Considering that juveniles can be transported to deeper waters either when alive or after death, here we propose two causes for the observed high percentages of A-7 carapaces. In the case of being transported alive, unfavorable conditions (e.g., low oxygen, low temperature) in the deep waters would cause high mortality and thus high abundance of their carapaces. In the case of post-mortem transport, an undisturbed environment would favor the preservation of carapaces and result in high frequency of A-7 carapaces. Therefore, the high frequency of A-7 carapaces may represent either biological processes or taphonomic bias, or a combination of both.

Given the low number of A-8 specimens in the samples, the high frequency of their carapaces is unexpected (Fig. 8). In fact, almost all the A-8 specimens are found as tightly enclosed carapaces rather than single valves. From some of them, tips of limbs can be seen protruding from the gaps of the valves. We suspect that most of the A-8 specimens recovered are living or recently dead; it is possible that A-8 juvenile valves are degraded quickly after they die and also after the valves are molted, and only very 'fresh' A-8 specimens can be recovered. Another possibility is that the very early juveniles, such as A-8 specimens, may have a different hinge structure from the later instars, which makes their valves less easily disarticulated. Zhang & Pratt (1993) suggested that Ostracoda had evolved from a univalved ancestor, and that the univalved character is retained in the early juveniles of some extant ostracods. Considering the fact that the body of the earliest juveniles of ostracods, especially their poorly calcified carapaces, have not been examined to exhaustive details (e.g., Smith & Martens, 2000; Kornicker et al., 2010), A-8 juveniles of *L. inopinata* may possibly have a dorsal structure that is different from the true hinge.

Conclusion

The instar composition, preservation of valve remains, and the presence of carapaces, of the widespread ostracod *Limnocythere inopinata* in the surface sediments are investigated in three large brackish lakes in northern China. Our data provide new understandings on the taphonomy of ostracods that have the potential to be extended to other meio-benthos such as chironomids. This study has important implications for the application of the microfossils in paleontological and paleoenvironmental researches.

Valve remains of *L. inopinata* in the surface sediments display significant size sorting across the lakebed, with younger juveniles preferentially deposited in deeper waters while older instars being in excess in shallower waters. Such a pattern matches the within-lake gradient of hydraulic instability and provides strong evidence of the occurrence of valve-remains transport in lakes. We suggest that after molting, and also after individual mortality, ostracods, especially the early juveniles, are relocated from shallower waters toward the deeper waters. Such transport greatly lessens, or ceases, at a threshold depth determined by the hydraulic conditions. Magnitude and pattern of valve-remains transport vary among lakes, and wind-driven hydrodynamics probably plays a major role in the lakes studied. Our study supports, but also improves upon the findings of earlier works by Whatley (1983, 1988) and Zhai et al. (2013).

Degradation of the valve remains of *L. inopinata* in the surface sediments of brackish lakes takes place mainly in the form of physical breakage. Changes in the degree of mechanical breakage of *L. inopinata* are complex, both spatially and among different instars. Sedimentation rate and hydraulic stability are the main causes for the observed inter-lake differences. However, we do not think the process of transport can cause substantial damage, since the transported juveniles are comparatively well preserved in all the lakes. Our data do not support the conclusion that smaller and thinner valves are more seriously damaged during the early taphonomic stage. Spatio-temporal changes in sedimentation rate and hydraulic stability, and the life cycle of ostracods may be responsible for the complex pattern of valve damage observed.

In order to better understand ostracod taphonomy, future researches should focus on more species and more types of limnic systems (in this paper all the lakes studied are brackish and alkaline). Not only physical damage, but also other kinds of degradation should be investigated.

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