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OSTRACODA – BIOSTRATIGRAPHY AND APPLIED ECOLOGY

Sediment penetration depths of epi- and infaunal ostracods from Lake Geneva (Switzerland)

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Abstract Many (palaeo-)environmental parameters can be deduced from ecological and chemical analyses of ostracods. However, the specific ecology of each taxon has a great impact on its reaction to changing environmental conditions. As a consequence, each taxon records these changes differently. The mean penetration depth (MPD) and relative individual abundances have been documented along sediment depth profiles for the dominant sub-littoral to profundal species of ostracods in western Lake Geneva, Switzerland, and this data can be used to estimate their preferential habitat in terms of sediment depths. *Isocypris*

beauchampi, *Limnocytherina sanctipatricii*, *Cypria ophthalmica* forma *lacustris* at 13-m water depths, *Limnocythere inopinata*, and a winter generation of *Herpetocypris reptans* have the shallowest habitat preferences at the study sites (MPDs of 0.45, 0.48, 0.49, 0.60, and 0.81 cm, respectively). These results suggest that these populations may be regarded as being preferentially epifaunal forms. Populations of *Cytherissa lacustris* (MPDs of 0.61, 0.73, and 0.82 cm at 13-, 33-, and 70-m water depths, respectively), *Cypria ophthalmica* forma *lacustris* at 70 m (MPD = 0.96 cm), *Fabaeformiscandona caudata* (MPD = 0.99 cm), and a summer generation of *Herpetocypris reptans* (MPD = 1.03 cm) were identified as being infaunal. *Candona neglecta* is the species that was found the deepest in the sediment of Lake Geneva, with MPDs of 0.65, 1.22, and 1.30 cm at 13-, 33-, and 70-m water depths, respectively. Information on the sediment texture and oxygen concentrations inferred from the analyses of sediment pore water suggest that the oxygen content of the sediment pore water is not the only dominant parameter controlling the differences in ostracod sediment penetration depths observed among the different sites, but that they might also be influenced by the sediment ‘softness,’ which itself depends on grain size, water content, and the abundance of organic matter in sediment.

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Introduction

Ostracods have proven useful for environmental or palaeoenvironmental studies. The absence or presence of different species, their individual morphological characteristics, and geochemical information related to their shells are strongly controlled by the environmental conditions prevailing during the development of these organisms. Therefore, it is possible to use fossil or modern ostracods to reconstruct different environmental parameters, such as water and/or air temperature (Dwyer et al., 1995; Viehberg, 2006; Horne, 2007), the oxygen content of water (Delorme, 1978; Geiger, 1993; Ricketts et al., 2001), water quality (Külköylüoğlu, 2004), the type and salinity of water (Curry, 1999; Boomer & Eisenhauer, 2002; Smith & Horne, 2002; Mezquita et al., 2005), the isotopic composition of water (von Grafenstein, 2002; Schwalb, 2003; Belis & Ariztegui, 2004), and the major, minor, and trace element levels in water, such as those of Mg, Sr, and U (De Deckker et al., 1988; Engstrom & Nelson, 1991; Yu et al., 2002; Janz & Vennemann, 2005; Tütken et al., 2006; Anadón et al., 2008).

Each taxon, however, has its own ecological characteristics. Therefore, analysis of ostracods often only provides information on the environmental conditions of sometimes very restricted microhabitats in a given period of the year. Thus, each taxon records the environmental characteristics according to its (micro-)habitat preference (epibenthic, epifaunal, or infaunal) and its specific life-cycle (such as permanent or summer forms). As a result, it is important to understand these ecological characteristics to appreciate which parameters can be deduced from the analysis of each taxon and to estimate the limits of the analysis (e.g. Ito & Forester, 2009). Despite the importance of such ecological characteristics, data on the preferential micro-habitats of the different taxa associated with these analyses are scarce, making ecological and geochemical interpretations difficult.

In this study, the ostracod sediment penetration depth in freshwater Lake Geneva, western Switzerland, was investigated with the aims of classifying the different species at the study site as epifaunal or infaunal forms and discussing the different parameters that might control the ostracod sediment penetration depth.

Materials and methods

Study site

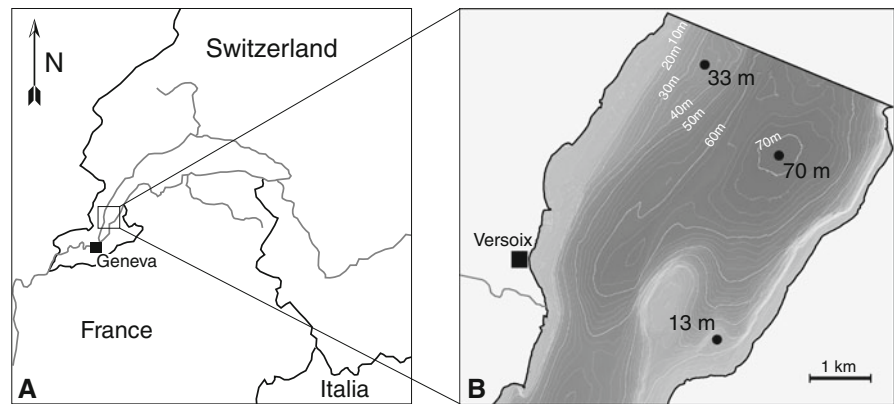
This study was carried out in the ‘Petit-Lac,’ which is the smaller western sub-basin of Lake Geneva. It is an oligo- to mesotrophic freshwater basin (3 km³), and its maximum depth is 72 m. This sub-basin presents monomictic behaviour, with the water column being totally mixed during winter overturning. In addition, deep currents induced during strong wind periods regenerate the deep water periodically during the year. Owing to these dynamic characteristics, the deep water oxygen content remains relatively high throughout the year in the ‘Petit-Lac’ (minimal values during the sampling period = 7.9 mg O₂/l, corresponding to an oxygen saturation level of 67%), which was even true during the highest anthropogenic nutrient overload period (minimal values from 1957 to 2007 = 6.04 mg/l; pers. com., Commission Internationale pour la Protection des Eaux du lac Léman, CIPEL). More information on Lake Geneva, the ‘Petit-Lac’ and the sampling site characteristics can be found in Decrouy et al. (subm. Sept. 2010a).

Three prerequisites were decided upon for the selection of the sampling sites. First, the sediments must be fine enough to allow a short gravity corer to be used to collect undisturbed sediment. Second, the incline must be low to facilitate sampling at a given water depth. Third, the sites must represent a profile from the littoral zone to the deepest part of the basin. Given these constraints, three sites, at 13-, 33-, and 70-m water depths, were selected for ostracod sampling (Fig. 1). In these sites, the sediments consist largely of sand, silt, and clay, and short cores (<1 m long) could easily be collected using a short gravity corer.

Sediment characteristics

The sediments at 13-, 33-, and 70-m water depths consist of authigenic and detrital calcium carbonate, silt, clay, sand, and organic matter. Overall, the sediment grain size decreased with water depth (silty-sand at 13 m and clayey-silt at 33 and 70 m; Vernet et al., 1972); the water content increased with water depth (85 wt% at 13 m, 93 wt% at 33 m, and 95 wt% at 70 m); and the organic matter increased with water depth (1.4% total organic carbon TOC at 13 m, 2.9%

Fig. 1 Geographical setting of Lake Geneva and sampling sites



TOC at 33 m, and 3.3% TOC at 70 m). Differences in the sediment characteristics among the three sites were also visually observed: at 13 m, the upper sediment layer was grey-brown and became darker at approximately 5–20 cm below the sediment–water interface, exhibiting a ‘granular’ aspect. In contrast, the upper sediment layer at 33 and 70 m was mostly brown, had a ‘jelly-like’ aspect, and became darker at approximately 3–10 cm below the sediment–water interface. Overall, the sediment appears to be softer with increasing water depth. Methods for sampling of sediments, analytical measurements, and a further discussion on sediment characteristics can be found in Decrouy et al. (subm. Sept. 2010a).

Ostracod sampling

The three study sites were visited on a monthly basis during a 1-year cycle. Depending on meteorological conditions, 2–5 short cores (<1 m) were recovered per site using a gravity corer. Once retrieved on board with the help of an electronic winch, the cores were directly mounted on a tripod equipped with a piston that raises the sediment in the core tube by 5 mm. Using this device, each core was sub-sampled in sediment slices of 0.5 cm for the two 2 cm of sediment and slices of 1 cm at 2–5-cm depth. Each subsample of sediment was placed in a flask closed with a pierced lid, stored during transport to the laboratory of the University of Lausanne in a cold box, and refrigerated at approximately 6°C until further processing.

To accelerate and facilitate ostracod separation, samples were washed in a 200- μ m mesh sieve.

Residues were transferred with tap water into Petri dishes. Living ostracods were collected using Pasteur pipettes under a stereomicroscope and killed in 30% alcohol. The animals were then stored in pure ethanol. All the samples were processed within 24–48 h, or rarely 72 h, after sampling.

For each sub-sample, the species and abundance of adults and juveniles (from A-4 to A-1 instars) were identified; when easily discernable, gender was also established for adults and A-1 instars. For further analyses of these data, each individual was assigned a sediment penetration depth corresponding to 0.25 if it was found between the 0- and 0.5-cm sediment interval, 0.75 if it was found between 0.5 and 1 cm, and so on. Thus, the sediment penetration depth estimated for each individual (‘individual sediment penetration depth’) corresponds to one number from the following list: 0.25, 0.75, 1.25, 1.75, 2.5, 3.5, or 4.5 cm.

In practice, the water–sediment interface of many cores was oblique to strongly disturbed, but non-disturbed horizontal water–sediment interfaces were also observed. Using the piston to extract the sediment, the ‘horizontality’ of the water–sediment interface has an impact on the accuracy and the precision of the individual sediment penetration depth determined for each individual found in the core. Each core was, therefore, given a label ranging from 1 to 4; with 1 representing a strongly perturbed water–sediment interface; 2 an oblique water–sediment interface; 3 a slightly oblique water–sediment interface; and 4 a horizontal water–sediment interface. In addition, for the purpose of a parallel study, several measurements were carried out directly in

the core (pH and temperature in supernatant water, and sediment pH profile). Some of these measurements required more time than others and, for some cores, no measurements were made at all. Hence, the time elapsed after a core was recovered on board until the end of its sub-sampling was different for each core. To estimate the effect of the time used to sub-sample the sediment on the ostracod sediment penetration depth, another label was given to each core according to the rapidity with which the core was sub-sampled. Label 4 indicates a core that was sub-sampled very rapidly (3–5 min), whereas label 1 indicates a core that was sub-sampled slowly (>15 min).

In summary, each core is characterised by two labels (A/B); the first of these (A) gives information on the rapidity of the sub-sampling and the second (B) on the quality of the water–sediment interface. Thus, a core labelled 4/4 had a horizontal water–sediment interface and was sub-sampled rapidly, whereas a core labelled 1/1 had a strongly disturbed water–sediment interface and was sub-sampled very slowly. Ideally, only cores labelled 4/4 should be used. However, the numbers of 4/4 cores were relatively low, and the numbers of specimens in these cores used to calculate individual penetration depth were likely to be too low, particularly for relatively rare species. Therefore, only data from cores labelled as 4/4, 4/3, 3/4, and 3/3 were selected for the examination of individual penetration depth. The data set resulting from this compilation is referred to as the ‘Selected’ data set and forms the principal data set of the present study. To examine the effect of storing and manipulating the cores on board before sub-sampling, data from the cores labelled 1/4, 1/3, 2/4, and 2/3 were regrouped and form a second data set referred to as the ‘Slow’ data set.

The number of individuals (N), arithmetic mean individual penetration depth (MPD) and 95% confidence intervals (CI) were calculated independently for each instar, each species, and each study site. The differences between genders, instars, collection sites, and ‘Selected’ and ‘Slow’ MPDs were tested using Student’s t -test when the variances of both data sets were similar, or a Welch–Aspin test when the variances were significantly different. The difference in variances was tested using an F -test.

Results

Ostracod systematics

Nine species were found alive at water depths between 13 and 70 m: *Candona candida* (O.F. Müller, 1776); *Candona neglecta* Sars, 1887, *Fabaeformiscandona caudata* (Kaufmann, 1900); *Cyprina ophthalmica* forma *lacustris* (Jurine, 1820; noted in general as *C. ophthalmica* in the text); *Herpetocypris reptans* (Baird, 1835); *Isocypris beauchampi* (Paris, 1920), *Limnocythere inopinata* (Baird, 1843); *Limnocytherina sanctipatricii* (Brady & Robertson, 1869); and *Cytherissa lacustris* (Sars, 1863). The bathymetric distribution, population densities, and life-cycle observed for these species are discussed in other articles (Decrouy, 2009; Decrouy et al., in prep.).

Relative individual abundances along sediment depth profiles

Figure 2 presents the relative individual abundances along sediment depth profiles based on the ‘Selected’ data set. The left side of Table 1 presents the MPDs calculated for each instar at the three sites, which were also established on the basis of the ‘Selected’ data set. For *C. neglecta*, no statistically significant differences between male and female MPDs were found, and the data for males and females were, therefore, regrouped for further calculations. In general, the major proportion of individuals was found in the top 2 cm of sediment, and the MPDs ranged from 0.25 to 1.33 cm. Note that the theoretical minimal value for MPD is 0.25, even if the individuals were actually living on the surface of the sediment at the time of sampling.

Behaviour of ostracods during sediment sub-sampling

The MPDs for the ‘Slow’ data set (see above) are reported in the right side of Table 1. For all the species except *F. caudata*, the MPDs calculated for the ‘Slow’ data sets are generally higher than the MPDs calculated for the ‘Selected’ data sets (27 ‘Slow’ MPDs are higher than the ‘Selected’ MPDs for a total of 37 comparisons; while 19 are higher for 25 comparisons when $N \geq 10$). The significance of

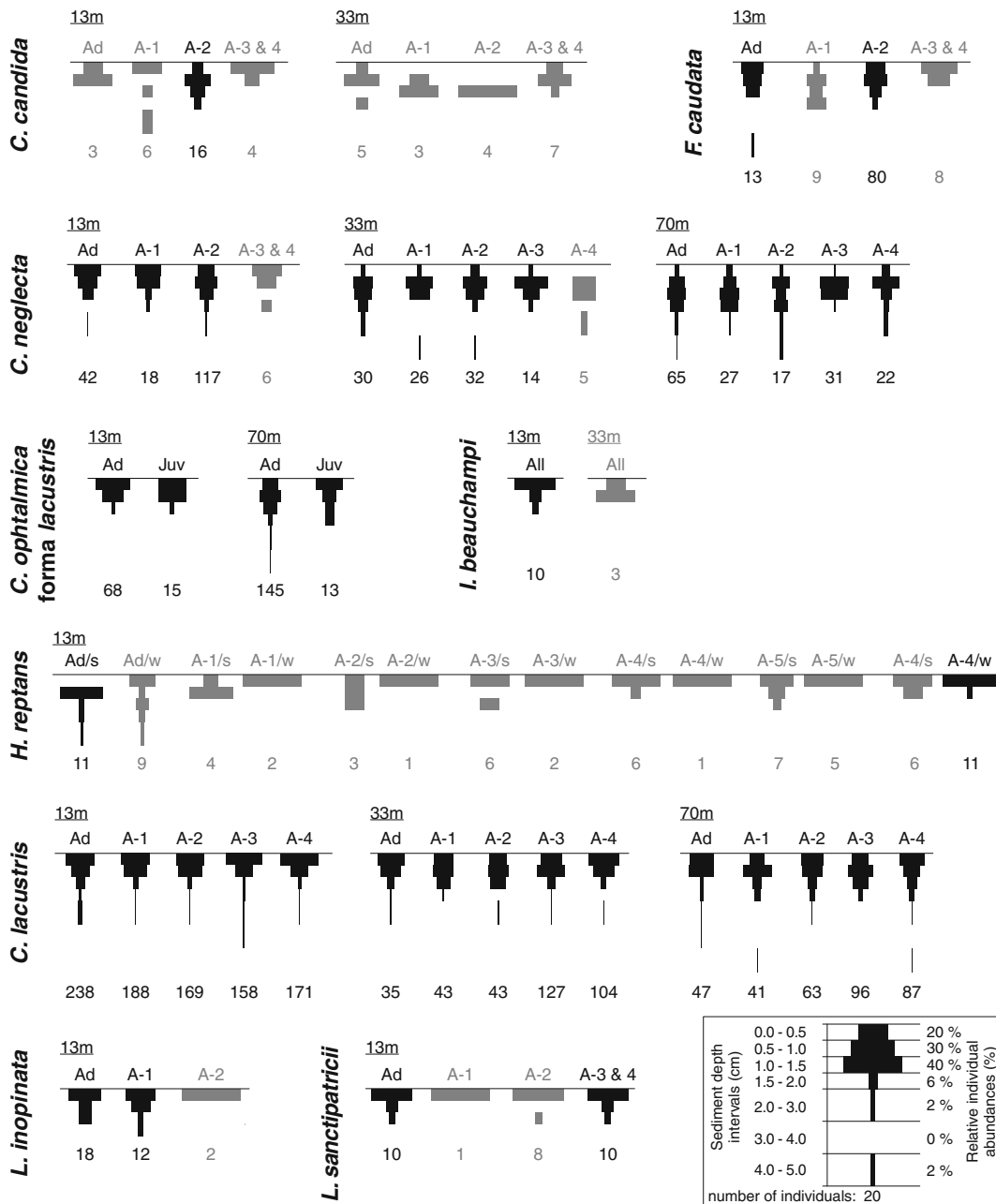


Fig. 2 Relative individual abundances along sediment depth profile for the ‘Selected’ data set (see text). Grey bars indicate differences in the MPDs between the ‘Slow’ data set and ‘Selected’ data set is indicated as follows in Table 1: for $P < 0.1$, the ‘Slow’ MPDs are noted in bold; for $P < 0.05$, the ‘Slow’ MPDs are noted in bold with an *; for $P < 0.01$, the ‘Slow’ MPDs are noted in bold with **; for $P < 0.001$, the ‘Slow’

adults of the Summer generation, *Ad/w* for adults of the Winter generation. The same labelling is used for the juvenile instars

the differences in the MPDs between the ‘Slow’ data set and ‘Selected’ data set is indicated as follows in Table 1: for $P < 0.1$, the ‘Slow’ MPDs are noted in bold; for $P < 0.05$, the ‘Slow’ MPDs are noted in bold with an *; for $P < 0.01$, the ‘Slow’ MPDs are noted in bold with **; for $P < 0.001$, the ‘Slow’

MPDs are noted in bold with ***; and when the N of one of the two data sets is < 10 , the ‘Slow’ MPDs are in brackets. The ‘Slow’ MPDs are not indicated for a $N < 2$. Eighteen ‘Slow’ MPDs were found to be higher at $P < 0.1$ than the ‘Selected’ MPDs of the 37 comparisons available (14 were higher for 25

Table 1 Arithmetic mean of individual sediment penetration depth (MPD), number of individuals used for calculation (*N*), and 95% confidence interval (CI) for ‘Selected’ and ‘Slow’ data set (see text)

Species and sites		‘Selected’ (4/4 4/3 3/4 3/3)						‘Slow’ (1/4 2/4 1/3 2/3)					
		Ad	A-1	A-2	A-3	A-4	A-5	A-6	Ad	A-1	A-2	A-3	A-4
<i>C. candida</i>													
13 m	<i>N</i>	3	6	16	4 ^a				–	–	4	–	
	MPD	0.58	1.17	0.91	0.38				–	–	(1.44*)	–	
	CI	0.72	1.16	0.25	0.40				–	–	1.19	–	
33 m	<i>N</i>	14	3	4	7 ^a				–	–	–	–	
	MPD	0.85	1.08	0.75	0.68				–	–	–	–	
	CI	0.68	0.72	0	0.32				–	–	–	–	
<i>C. neglecta</i>													
13 m	<i>N</i>	42	18	117	6 ^a				17	8	33 ^a		
	MPD	0.66	0.64	0.87	0.67				0.88	(0.97)	1.11		
	CI	0.15	0.22	0.10	0.61				0.30	0.56	0.63		
33 m	<i>N</i>	30	26	32	14	5			28	18	24	14	7
	MPD	1.27	1.16	1.01	0.93	1.30			1.26	1.00	1.22	1.11	(1.04)
	CI	0.24	0.35	0.22	0.22	0.89			0.29	0.18	0.21	0.14	0.45
70 m	<i>N</i>	65	27	17	31	22			18	8	11	3	
	MPD	1.33	1.22	1.59	0.99	1.10			1.60	(1.00)	1.86	(1.33)	
	CI	0.17	0.22	0.48	0.11	0.31			0.33	0.32	0.45	2.51	
<i>F. caudata</i>													
13 m	<i>N</i>	13	9	80	–	–			3	12	–	–	
	MPD	0.88	1.14	0.78	–	–			(0.58)	0.83	–	–	
	CI	0.53	0.42	0.10	–	–			1.43	0.35	–	–	
Summer <i>H. reptans</i>													
13 m	<i>N</i>	11	4	3	6	6	7	3	3	2	–	–	–
	MPD	1.05	1.00	0.75	0.58	0.33	0.54	0.42	(1.67)	(1.88)	–	–	–
	CI	0.39	0.80	1.24	0.54	0.21	0.36	0.72	2.18	–	–	–	–
Winter <i>H. reptans</i>													
13 m	<i>N</i>	9	2	1	2	1	5	11	–	2	–	–	3
	MPD	0.94	0.25	0.25	0.25	0.25	0.25	0.30	–	(0.75)	–	–	(0.58)
	CI	0.62	–	–	–	–	0	0.10	–	–	–	–	0.72
<i>L. inopinata</i>													
13 m	<i>N</i>	18	12	2	–	–							
	MPD	0.58	0.63	0.25	–	–							
	CI	0.21	0.31	–	–	–							
<i>L. sanctipatricii</i>													
13 m	<i>N</i>	10	1	8	10 ^a								
	MPD	0.45	0.75	0.63	0.30								
	CI	0.25	–	0.37	0.11								
<i>C. lacustris</i>													
13 m	<i>N</i>	238	188	169	158	171			78	69	63	40	19
	MPD	0.64	0.60	0.62	0.53	0.47			0.89***	0.82**	0.95***	0.86***	0.84**
	CI	0.06	0.06	0.07	0.07	0.05			0.12	0.15	0.17	0.16	0.25

Table 1 continued

Species and sites		'Selected' (4/4 4/3 3/4 3/3)						'Slow' (1/4 2/4 1/3 2/3)					
		Ad	A-1	A-2	A-3	A-4	A-5	A-6	Ad	A-1	A-2	A-3	A-4
33 m	<i>N</i>	35	43	43	127	104			39	32	48	83	98
	MPD	0.71	0.75	0.80	0.69	0.55			1.01*	0.95*	0.79	0.74	0.73***
	CI	0.20	0.13	0.16	0.08	0.07			0.25	0.15	0.12	0.08	0.09
70 m	<i>N</i>	47	41	63	96	87			10	8	19	33	38
	MPD	0.74	0.91	0.76	0.79	0.78			1.00	(1.66*)	0.86	0.79	0.72
	CI	0.19	0.27	0.13	0.09	0.14			0.39	0.68	0.31	0.17	0.19
<i>C. ophthalmica</i> forma <i>lacustris</i>									Ad	Juv			
	<i>N</i>	68	15						29	–			
13 m	MPD	0.49	0.55						0.66	–			
	CI	0.07	0.18						0.24	–			
70 m	<i>N</i>	145	13						6	3			
	MPD	0.96	0.75						(0.67)	(1.00)			
	CI	0.12	0.35						0.39	3.23			
<i>I. beauchampi</i>		All											
13 m	<i>N</i>	10											
	MPD	0.45											
	CI	0.25											
33 m	<i>N</i>	3											
	MPD	0.58											
	CI	0.72											

Significance of the difference between 'selected' data and 'slow' data is represented as follows: 'bold MPDs' means that significance test calculated for the difference between 'Selected' MPDs and 'Slow' MPDs give $P < 0.10$

* is added to 'Slow' MPDs when $P < 0.05$; ** when $P < 0.01$, *** when $P < 0.001$ (see text)

^a A-3 and A-4 instars regrouped to increase the number of individuals for calculations

comparisons for $N \geq 10$) and ten at $P < 0.05$ (8 for $N \geq 10$). The difference between the 'Slow' MPDs and the 'Selected' MPDs was particularly evident for *C. lacustris* at 13-m water depth. Given the errors produced by the quality of coring (data obtained from cores having a slightly disturbed or inclined sediment–water interface were taken into account), the effects of the coring itself on the distribution of ostracods (dragging down of sediment along the tube as it was introduced into the sediment), the punctual measurements of individual penetration depths for a pattern that is expected to be continuous (only four slices of 0.5-cm thickness each contain the majority of all individuals), and the uncertainty of sediment slice thickness (the piston system is rudimentary), the differences between the MPDs having a level of significance of $P < 0.1$ might reflect a real change in

the depth distribution of the individuals. In addition, MPD calculations do not reflect all types of variations in individual distributions, such as an increase of variance without significant variations of the arithmetic mean.

Seasonal change in habitat depth

Measurements of the carbon and oxygen isotope compositions performed on the shells of the living individuals collected during this study suggest that the species *H. reptans* produce two generations per year at a 13-m water depth. In addition, these measurements indicate that the two generations must have calcified their valves in different microhabitats: the shells of the summer generation appear to be in equilibrium with sediment pore water, suggesting that

these individuals lived within the sediment, whereas the shells of the winter generation appear to be in equilibrium with bottom water, suggesting that these individuals lived mainly on the surface of the sediment, or immediately below the water–sediment interface (Decrouy, 2009; Decrouy et al., subm. Sept. 2010b). To test these assumptions, the data for *H. reptans* were divided into two data sets, one for individuals collected from July to November, referred to here as the ‘summer’ *H. reptans* population, and another one for individuals collected from December to June, referred to here as the ‘winter’ *H. reptans* population. For all the instars, the MPDs are lower for the summer generation compared to that for winter (Table 1). The individual distributions along the sediment depth illustrated in Fig. 2 suggest the same behaviour, with the majority of the winter individuals found in the first 0.5 cm, whereas individuals of the summer generation are found deeper in the sediment. The significances of the differences between the MPDs of the two generations were tested, and the results are presented in Table 2. Because only a few individuals were collected, the data for the Adults and A-1 (‘Ad + A-1’) were regrouped. The data for A-2 and A-3 (‘intermediate juveniles’) and A-4 through A-6 (‘younger juveniles’) were also regrouped. The differences between the summer and winter MPDs were found to be significantly different between the intermediate juveniles and the younger juveniles. However, the significance of the difference between the ‘Ad + A-1’ MPDs was found to be low ($P = 0.21$). The principal components analysis (PCA) computed for the relative ‘Ad + A-1’ individual abundances along the sediment depth profiles

Table 2 Results of significance tests, given as P , between MPDs calculated for summer and winter generations of *H. reptans*

Instars	Summer versus winter
Ad + A-1	0.21
A-2 + A-3	(*)
YJ (A-4, 5 & 6)	*

‘Bold numbers’ for $P < 0.10$; * for $P < 0.05$; ** for $P < 0.01$; *** for $P < 0.001$

Numbers were put in brackets when significance tests were effectuated with $N < 10$ in one of the two data sets or in both data sets. A-3 & 4 means that data for A-3 and A-4 development stages were regrouped to increase numbers of individuals for calculations

indicates that the distributions of both generations along the sediment depth profile are different (see elsewhere). This discrepancy can be explained by the fact that the MPDs of both data sets are relatively similar (MPD = 1.03 ± 0.52 for the summer generation compared to MPD = 0.81 ± 0.30 for the winter generation), but the distributions of individuals along the sediment depths are different: 73% of the summer ‘Ad + A-1’ individuals are found between 0.5 and 1 cm below the sediment–water interface, whereas 55% of the winter ‘Ad + A-1’ individuals are found between 0 and 0.5 cm. Hence, given that (1) the summer MPDs are higher for all the instars compared with the winter MPDs; (2) the difference is significant for ‘intermediate juveniles’ and ‘younger juveniles’; (3) the PCA clearly separates the two generations for ‘Ad + A-1’ individuals; and (4) the stable isotope compositions of the shells indicate two different types of microenvironments for the two generations, we suggest that there is a difference in the microenvironment preferences of the two generations. Note that seasonal changes of individual penetration depths were not observed for the other species.

Relationship between individual penetration depth and ostracod ontogenesis

The results in the left side of Table 1 and in Fig. 2 suggest that individual penetration depths increase with ostracod ontogenesis, i.e. the penetration depth is low for young juveniles and is higher for adults. The significance in the differences between instar MPDs was generally low to nonexistent when consecutive instars were compared (i.e. instars separated by a single moulting, such as ‘Ad’ compared to ‘A-1’), but this significance increased as the adult MPDs were compared with the younger juvenile MPDs (Table 3). This finding is in agreement with a gradual increase of the individual penetration depth with ontogeny, with the difference between the MPDs of two consecutive instars being too small to be detected by the sampling method used here.

The MPD found for A-2 individuals belonging to *C. neglecta* at 13-m depth seems to deviate from this model. The MPD found for this developmental stage is significantly higher than the MPDs calculated for the other instars belonging to the same species collected at the same site (Table 3), suggesting that for this population (i.e. *C. neglecta* at 13-m), the

Table 3 Results of significance tests (Student’s *t*-test or Welch–Aspin test, see text), given as *P*, between MPDs calculated for each development stage (e.g. Ad vs. A-1, Ad vs. A-1, etc.)

Instar versus instar (<i>P</i>)						Instar versus instar (<i>P</i>)					
<i>C. candida</i>						Summer <i>H. reptans</i>					
13 m	A-1	A-2	A-3 & 4			13 m	A-2 & 3	A-4, 5 & 6			
Ad	(0.21)	(0.14)	(0.18)			Ad & A-1	(*)	***			
A-1		(0.30)	(0.07)			A-2 & 3		(0.11)			
A-2			(*)			Winter <i>H. reptans</i>					
33 m	A-1	A-2	A-3 & 4			13 m	A-2 & 3	A-4, 5 & 6			
Ad	(0.26)	(0.37)	(0.26)			Ad & A-1	(*)	*			
A-1		(*)	(0.06)			A-2 & 3		(0.16)			
A-2			(0.34)			<i>L. inopinata</i>					
<i>C. neglecta</i>						13 m	A-1				
13 m	A-1	A-2	A-3 & 4			Ad	0.40				
Ad	0.44	*	(0.49)			<i>L. sanctipatricii</i>					
A-1		*	(0.45)			13 m	A-2	A-3			
A-2			(0.19)			Ad	0.18	0.12			
33 m	A-1	A-2	A-3	A-4	A-3 & 4		A-2	*			
Ad	0.31	0.06	*	(0.46)	0.09		<i>C. lacustris</i>				
A-1		0.21	0.12	(0.37)	0.25		13 m	A-1	A-2	A-3	A-4
A-2			0.3	(0.17)	0.46		Ad	0.21	0.33	*	***
A-3				(0.08)			A-1		0.38	0.06	***
70 m	A-1	A-2	A-3	A-4	A-3 & 4		A-2			*	***
Ad	0.24	0.10	**	0.09	**		A-3				0.10
A-1		0.08	*	0.25	*		33 m	A-1	A-2	A-3	A-4
A-2			*	*			Ad	0.36	0.24	0.45	0.08
A-3				0.25			A-1		0.32	0.23	**
<i>F. caudata</i>						A-2			0.11	**	
13 m	A-1	A-2	A-3 & 4			A-3				**	
Ad	(0.23)	0.33	(0.05)			70 m	A-1	A-2	A-3	A-4	
A-1		(*)	(**)			Ad	0.14	0.42	0.33	0.37	
A-2			(*)			A-1		0.16	0.18	0.16	
<i>C. ophthalmica</i>						A-2			0.38	0.43	
13 m	Juv					A-3				0.46	
Ad	0.23					Summer <i>H. reptans</i>					
13 m	A-1	A-2	A-3	A-4	A-5	A-6					
Ad	(0.45)	(0.22)	(0.06)	(**)	(*)	*					
A-1		(0.27)	(0.12)	(**)	(0.06)	(0.07)					
A-2			(0.33)	(0.05)	(0.24)	(0.19)					
A-3				(0.15)	(0.43)	(0.31)					
A-4					(0.14)	(0.31)					
A-5						(0.33)					

‘Bold numbers’ for *P* < 0.10; * for *P* < 0.05; ** for *P* < 0.01; *** for *P* < 0.001

Numbers were put in brackets when significance tests were effectuated with *N* < 10 in one of the two data sets or in both data sets. A-3 & 4 means that data for A-3 and A-4 development stages were regrouped to increase numbers of individuals for calculations

microenvironment preferences of the A-2 instars differ from the general behaviour observed for this species.

Differences in individual penetration depths among the three study sites

The results presented in the left side of Table 1 and in Fig. 2 suggest that individual penetration depth increases with water depth, i.e. individuals are found deeper in the sediment at the deeper water sites (33 and 70 m) compared to the sediment depth at which individuals are found in 13-m water depths. The significance tests between the MPDs calculated for the different sites support the observation that the MPDs are generally higher at 33 and 70 m compared to the MPDs found at 13 m, but they are mostly similar when the MPDs for 33 m are compared to the MPDs found at 70 m (Table 4).

Classification of the different populations

Because the MPDs found for the Ad and A-1 development stages were not different (Table 4), the data of both development stages were regrouped to increase the number of individuals when attempting to classify the different populations in terms of habitat

depth. To achieve this classification, three methods were used. The first method uses a simple ranking of the MPDs. The second method consists of a principal component analysis (PCA) using the first two principal components (>76% of variance) and cluster analyses with Euclidian distance and Ward agglomeration algorithms performed on the relative individual abundances along the sediment depth profile (Fig. 3). The third method considers only the relative individual abundances found in the top 0.5 cm of sediment: a threshold $\geq 50\%$ of individuals found in the top 0.5 cm of the sediment was arbitrarily chosen to distinguish populations with the highest individual abundance in the top 0.5 cm compared to the other populations (see 'Discussion' section; Fig. 4). The results obtained from the three methods suggest that the populations of *I. beauchampi*, *L. sanctipatricii*, *L. inopinata*, winter *H. reptans*, and *C. ophthalmica* at 13 m have the more surficial habitat preferences (Table 5). In contrast, the populations of *C. neglecta* at 33 and 70 m have a deeper habitat preference. The populations of *C. lacustris*, *F. caudata*, *C. neglecta* at 13 m, and *C. ophthalmica* at 70 m rank in-between the two extremes. The results for *C. candida* indicate a relatively deep habitat compared to the habitat found for the other populations at the same site. However, the low number of individuals of this species might hint at

Table 4 Results of significance tests, given as *P*, between MPDs calculated for each development stage at the three different sites (e.g. Ad 13 m vs. Ad 33 m, Ad 13 m vs. Ad 70 m, etc.)

'Bold numbers' for $P < 0.10$; * for $P < 0.05$; ** for $P < 0.01$; *** for $P < 0.001$

Numbers were put in brackets when significance tests were effectuated with $N < 10$ in one of the two data sets or in both data sets. A-3 & 4 means that data for A-3 and A-4 development stages were regrouped to increase numbers of individuals for calculations

Species	Instars	13 m vs. 33 m	13 m vs. 70 m	33 m vs. 70 m
<i>C. candida</i>	Ad	(0.24)		
	A-1	(0.45)		
	A-2	(0.26)		
	YJ	(0.08)		
<i>C. neglecta</i>	Ad	***	***	0.34
	A-1	**	***	0.39
	A-2	0.12	**	**
	A-3			0.28
	A-4			(0.29)
	YJ	(0.23)	(*)	0.47
<i>C. ophthalmica</i>	Ad		***	
	Juv		0.14	
<i>C. lacustris</i>	Ad	0.26	0.16	0.41
	A-1	*	*	0.14
	A-2	*	*	0.37
	A-3	**	***	0.06
	A-4	*	***	**

Fig. 3 PCA and cluster analysis obtained on relative ‘Ad + A-1’ individuals abundances along sediment depth profiles (see text). Grey symbols were used to represent populations for which more than 50% of ‘Ad + A-1’ individuals were found in the top 0.5 cm of sediment

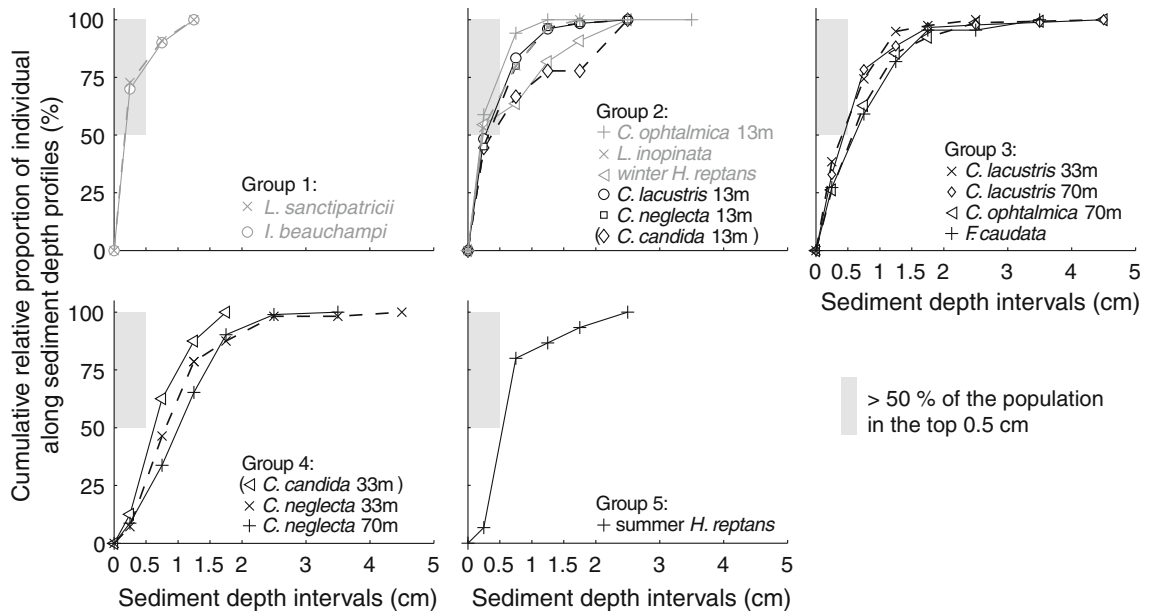
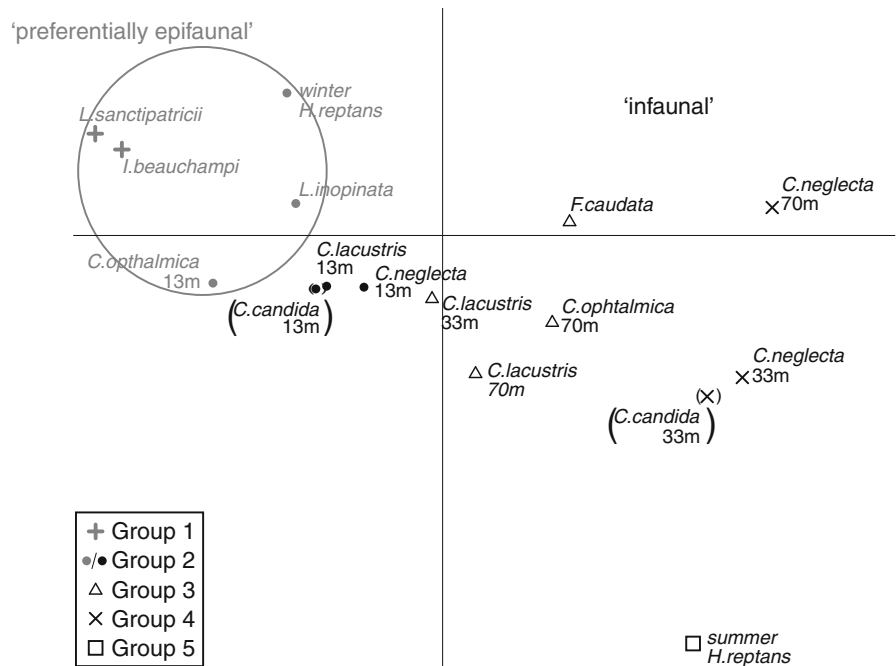


Fig. 4 Cumulative histograms of relative ‘Ad + A-1’ individual abundances along sediment depth profiles obtained for the different populations. Populations were regrouped according to the results of the PCA and cluster analysis. Grey symbols

were used to represent population for which more than 50% of the ‘Ad + A-1’ individuals were found in the top 0.5 cm of sediment

a more surficial habitat, and the results presented here must be treated with caution. The PCA suggests that the summer population of *H. reptans* have a different

behaviour than all of the other species, with high individual penetration depths and an atypical distribution of individuals along the sediment depth.

Table 5 Mean individual penetration depths (MPDs) calculated for ‘Ad + A-1’ and classification of the different populations in term of habitat preferences: ‘MPD rank’ stands for the ranking of the populations according to their respective MPDs, ‘PCA group’ stands for the regrouping obtained from PCA and cluster analysis, ‘>50% in 0–0.5 cm’ stands for populations having more than 50% of their individuals (‘Ad + A-1’) in the top 0.5 cm

Species	N	MPD	CI	MPD rank	PCA group	>50% in 0–0.5 cm
Preferentially epifaunal						
<i>I. beauchampi</i>	10	0.45	0.25	1	1	Yes
<i>L. sanctipatricii</i>	11	0.48	0.23	2	1	Yes
<i>C. ophthalmica</i> 13 m	68	0.49	0.07	3	2	Yes
<i>L. inopinata</i>	30	0.6	0.16	4	2	Yes
<i>H. reptans</i> winter	11	0.81	0.52	8	2	Yes
Infaunal						
<i>C. lacustris</i> 13 m	426	0.61	0.04	5	2	
<i>C. neglecta</i> 13 m	60	0.65	0.12	6	2	
<i>C. lacustris</i> 33 m	78	0.73	0.11	7	3	
<i>C. lacustris</i> 70 m	88	0.82	0.16	9	3	
<i>C. ophthalmica</i> 70 m	145	0.96	0.12	11	3	
<i>F. caudata</i> 13 m	22	0.99	0.34	13	3	
<i>H. reptans</i> summer	15	1.03	0.30	14	5	
<i>C. neglecta</i> 33 m	56	1.22	0.56	15	4	
<i>C. neglecta</i> 70 m	92	1.30	0.13	16	4	
<i>C. candida</i> 13 m	9	0.97	0.72	12	2	
<i>C. candida</i> 33 m	8	0.94	0.38	10	4	

Discussion

Ostracod behaviour during sediment sub-sampling

Our results indicate that ostracods tend to dig deeper as time passes during the sub-sampling of the cores. It is possible that the ostracods actually associate the disturbance of the environment during the sub-sampling with potential danger (perhaps predation). Burrowing into the sediment is known to be an effective strategy to reduce the risk of predation (Mbahinzireki et al., 1991). Therefore, the ostracods may actually try to escape predation by digging deeper into the sediment.

Owing to the potential ‘digging’ reaction during subsampling, the sediment penetration depths estimated for the different species in Lake Geneva cannot be directly interpreted as living depths, as they may be overestimated. Therefore, the MPDs illustrated here should only be used to compare the individual penetration depths between different development stages, species, or sites. In addition, these results should be interpreted as representing the potential digging ability of the specimen rather than as its true habitat depth. However, the MPDs and relative individual abundances along the sediment

depth profile calculated from the ‘Selected’ data set indicate that the majority of the individuals are found in the top 2 cm of the sediment, and these results are comparable to those of existing data (Danielopol et al., 1988; Griffiths & Martin, 1993; Corbari et al., 2004). Thus, the results of this study may still be used to study the general distribution of ostracods along sediment depths and to examine which parameters may influence this distribution.

Individual distribution along sediment depth profiles

Several studies have investigated ostracod sediment penetration depths. Geiger (1990) observed that the distribution of individuals of *Cytherissa lacustris* in sediments is determined by the redox conditions and, thus, by the oxygen concentrations in interstitial water. Most of the individuals collected were found in the uppermost layer of the sediment (0–1 cm), where the redox potential was high (>275 mV). Corbari et al. (2004) confirmed that ostracod depth distribution in the sediment was directly linked to the oxygen concentration. They found that specimens of *Leptocythere castanea* and *Cyprideis torosa* adjust their tissue oxygenation by migrating through the O₂ gradient within sediments to where the PO₂ of the

interstitial water is between 3 and 5 kPa. However, factors other than oxygen may influence the ostracod distribution in sediments. Ostracods can explore sediments in search of nutrients as shown by the behaviour of *Cypridopsis vidua* (Roca & Danielopol, 1991). Burrowing is also a very efficient measure of protection against predators, as described for *C. lacustris* (Mbahinzireki et al., 1991). This species also avoids contaminated sediments (Danielopol et al., 1990). In Lake Mondsee, it has also been suggested that factors such as the quality and texture of the substrate can restrain *C. lacustris* from burrowing and that depth penetration depends on the compactness of the sediment more than on its grain size (Danielopol et al., 1988). In addition, the depth of penetration seems to depend on the developmental stage of the ostracods: younger juveniles generally remain in the uppermost sediment layer, whereas older juveniles and adults are able to dig deeper (Danielopol et al., 1988, 1990). Lower survival at low oxygen concentrations and an inferior number of sieve pores of juveniles of *C. lacustris* suggest that younger specimens need higher amounts of oxygen, explaining their relatively shallow microhabitat compared to adults (Geiger, 1990).

Differences in sediment characteristics among the three study sites and variations along sediment depth profiles

Detailed knowledge of sediment characteristics at the different study sites and along the sediment depth profile is important to examine which factors might influence ostracod microenvironment preferences in terms of sediment habitat depths. As discussed in the preceding section, previous studies have suggested that the oxygen concentration in sediment pore water and sediment compactness may influence the depth at which ostracods are found in the sediment (Danielopol et al., 1988, 1990; Geiger, 1990; Corbari et al., 2004). Neither parameter was measured directly on site during this study; however, previous studies conducted on sediment characteristics in lacustrine environments, the general behaviour of oxygen concentrations along sediment depth profiles, and geochemical measurements carried out on sedimentary pore water in Lake Geneva provide sufficient information to infer the behaviour of oxygen concentrations in pore water and the sediment compactness

prevailing at the three sampling sites and to suggest which factors might influence the vertical distribution of ostracods within the sediment of Lake Geneva.

Owing to the remineralisation of sedimentary organic matter during microbial aerobic respiration, the concentration of oxygen in sediment pore water decreases along a sediment depth profile (e.g. Martin et al., 1998). This mechanism must be similar for the sediment of Lake Geneva, and a general decrease of the oxygen concentration in pore water along sediment depth profiles must be the rule. However, the rate of the decrease in oxygen concentration with sediment depth and the maximal oxygen penetration depth are unknown for the study sites. However, information about oxygen concentrations in sediments and the depth of anoxia in the sediment at the study sites can be deduced from other measurements performed on the sediment pore water of Lake Geneva. Bolliger et al. (1992) measured a sigmoid decrease of the nitrate and sulphate concentration in the sediment pore water of a short core taken at 250 m in the 'Grand-Lac' (principal basin of Lake Geneva). The nitrate concentrations reached zero between approximately 2 and 3 cm below the sediment–water interface, whereas the sulphate concentrations reached zero at approximately 8 cm below the sediment–water interface. In addition, those authors measured a sharp increase of the NH_4^+ concentration between 0 and 10 cm below the sediment–water interface. These results indicate that a reduction of sulphate and nitrate does occur in the first centimetre of the sediment of the Lake Geneva. In the same publication, those authors stated that the sediment is anoxic a few millimetres of the water–sediment interface surface. Brandl et al. (1990) measured an increase of methane concentration (from 0 mmol at the sediment–water interface to 0.8 mmol at 20 cm above sediment–water interface) in the pore water of a short core collected at the same site, which suggests that methanogenesis also occurs in the sediment of Lake Geneva. However, these measurements were carried out in the 'Grand-Lac', and this basin is known to undergo periodic depletions in the oxygen concentration of deep water (CIPEL, 1984, 2010). Under the assumption that the chemical composition of lake water and sediment characteristics are similar for both basins, sulphate and nitrate reduction as well as methanogenesis must also occur in the sediments found at the three study sites. However, as the 'Petit-Lac' is well oxygenated

throughout the year (CIPEL, 1984, 2006), the depth at which anoxic conditions are observed in the sediment of the ‘Grand-Lac’ cannot be transferred to the study sites located in the ‘Petit-Lac.’

A study based on the concentration of dissolved inorganic carbon (DIC) in interstitial pore water and its carbon isotope composition ($\delta^{13}\text{C}_{\text{DIC}}$), pore water Ca^{2+} concentration, and pH profiles along sediment depth suggested that the remineralisation of organic matter is mainly driven by both aerobic and anaerobic respiration, with the reduction of sulphate and nitrate in the top 5 cm of the sediment at 13- and 33-m water depth sites. The conditions are similar in the top 3 cm of sediment at the 70-m water depth site. Here, however, methanogenesis may already occur below 3 cm of the water–sediment interface. This finding also suggests that at 70-m water depth, methanogenesis occurs at shallower depths in the sediment than at the two shallower sites. In addition, the relative importance of the remineralisation of organic matter via the reduction of sulphate and/or nitrate increases with water depth at the expense of aerobic respiration (Decrouy et al., subm. Sept. 2010a). These results, together with field observations that sediments become darker closer to the water–sediment interface in deeper sites and that the measured increase in sediment organic matter content increases with water depth, suggest that the oxygen consumption rate may be higher in deep sites compared to shallow sites. Higher oxygen consumption results in a decrease in the oxygen penetration depth with increasing water depth. These interpretations are in agreement with the results of other studies, in which the decrease of the oxygen content of bottom water and the increase of organic matter within the sediment with increasing water depth were observed to lead to a lower penetration depth of oxygen in the sediment (Danielopol et al., 1990).

Owing to the increase of sediment organic matter content and water content, as well as the decrease of grain size with water depth, the sediment texture changes from a sediment that is mostly compact at a 13-m water depth to a sediment that is very soft at 33- and 70-m water depths. Visual inspection during sampling also support these results: at 33 and 70 m, the surficial sediments were easily shaken as the cores were handled on board, whereas the sediments from 13 m remained mostly motionless. Hence, the sediment compactness decreases with increasing water depth.

Overall, indirect measurements and cross-checking with other studies suggest the following pattern for the study sites: (1) the sediment at 13 m is more compact compared to the sediment at 33 and 70 m; (2) the oxygen concentration decreases along the sediment depth profile; and (3) the oxygen concentration in the sediment and oxygen penetration depth decrease with increasing water depth. These three assumptions form the basis of the following discussion focusing on the potential influence of sediment characteristics on the distributions of individuals along the sediment depth profiles found at the three study sites.

Variation of individual penetration depths during ontogenesis

For most of the investigated species, penetration depth increases as the individual moults from one developmental stage to the next. This behaviour was previously observed for *C. lacustris* and was attributed to a lower tolerance of the juveniles with regard to oxygen depletion (Geiger, 1990). However, von Grafenstein et al. (1996) suggested that in the abyssal zone of Lake Ammersee, Candoninae survive the summer oxygen depletion as A-2 juveniles before reaching maturity immediately after the overturn of the water column in winter. In the case of Lake Geneva, juveniles were generally found deeper in the sediment at 70 m compared with the site at 13-m water depth, suggesting that, for the three study sites, the differences in the vertical distribution of juveniles are not only related to the oxygen concentration of pore water but also to other factors. Juveniles gain new limbs at each moulting; at the same time, the limbs grow and become more sophisticated (see Meisch, 2000 for a short introduction to ostracod ontogeny). Having fewer and/or poorly developed limbs, juveniles are disadvantaged in comparison to adults when digging deeper into the more compacted sediments. In addition, as the compactness of the sediment decreases with increasing water depth, the sediment texture may allow juveniles to dig deeper into the sediment at 33 and 70 m compared to 13 m.

At 13-m water depth, A-2 individuals belonging to *C. neglecta* exhibit a different pattern since they were found deeper within the sediment than the rest of the instars living at the same site. At this site, the monthly mean water temperatures are higher than

12°C from July to October. During this period, all of the individuals that have reached the A-2 developmental stage halt their development and moulting in A-1, and finally, the adult stage occurs only when the water temperature decreases in autumn (Decrouy, 2009; Decrouy et al., in prep.). Viehberg (2006) calculated an optimum temperature of 7.6°C with a tolerance of $\pm 2.2^\circ\text{C}$ for *C. neglecta*. Accordingly, it has been suggested that the A-2 instars may enter into a type of resting stage to survive the warmest period of the year in shallow zones of lakes (Decrouy, 2009; Decrouy et al., in prep.). Corbari et al. (2005) suggested that Cylindroleberids rest during the daytime in self-made nests to breathe under hypoxic and hypercapnic conditions. Those authors added that the resulting physiological mechanisms should depress their metabolic activity during the daytime and help them to reach a type of torpor. Based on this study, it is suggested that A-2 instars belonging to *C. neglecta* adopt a similar behaviour at the 13-m water depth. That is, as the water temperature increases over a threshold temperature of approximately 12°C, individuals that have reached the A-2 developmental stage dwell deeper in the sediment where the oxygen concentration is lower, favouring a decrease in their metabolic activity. These individuals remain there as long as the water temperature is high, and once the water temperature returns to tolerable levels, they regain their usual habitat, resume their development, and rapidly reach adulthood. This behaviour is not observed at the 33- and 70-m water depths. The reason for this may be attributed to the fact that no breaks in individual development were observed at these depths because the monthly mean water temperature remains lower than 9°C throughout the year at 33- and 70-m water depths (Decrouy, 2009; Decrouy et al., in prep.).

Variation of individual penetration depths between study sites

Overall, individuals were found deeper in the sediment at 33- and 70-m water depths compared to the 13-m water depth. As discussed above, this pattern cannot be due to the oxygen concentration in pore water or the oxygen penetration depth because the individual penetration depths are the lowest in the 13-m depth site, which is expected to present higher oxygen penetration depths, whereas higher individual

penetration depths are found where the oxygen concentrations in pore water and the oxygen penetration depths are expected to be low (33 and 70 m). Hence, the sediment texture and its softness may actually be the dominant parameters influencing the differences in the distribution of individuals along the sediment depth profiles found between the study sites.

*Seasonal variation of the sediment penetration depth observed for *Herpetocypris reptans**

The reasons for the difference in the sediment depth habitats observed for the summer and winter generations of *H. reptans* are unclear. Food sources may, in part, explain this observation. Seasonal food availability, however, suggests the opposite behaviour. During summer, the supply of organic matter sinking from the epilimnion and settling on the surface of the sediment is higher. Thus, food availability is high at the surface of the sediment, and ostracods can obtain their food in relatively shallow micro-habitats. In contrast, the supply of organic matter from the superficial water is almost non-existent during winter. In addition, owing to water mixing during winter overturning, the oxygen concentration above the sediment is high, leading to a higher remineralisation of organic matter. Under these conditions, it may be preferable for ostracods to dig into the sediment, where remineralisation is lower and food availability is constant throughout the year. Higher predation and competition for resources during summer may, therefore, be the predominant factors that control the seasonal variability of sediment penetration depths for *H. reptans*.

Classification of the different populations

Suggesting a classification for the different species according to their microhabitat sediment depth preferences represents a difficult task. In general, benthic organisms are regarded as infaunal when individuals live in the sediment or epifaunal when individuals live on or above the sediment. However, as the sediment was sub-sampled in 0.5-cm slices, individuals found in the top 0.5 cm of the sediment may actually have lived on the surface of the sediment. Hence, the method used here is not able to distinguish forms that are living on the surface of the sediment, which should therefore be regarded as epifaunal,

from infaunal forms that are living between 0- and 0.5-cm sediment depths. Another approach, such as making direct observations of ostracods in micro-aquaria, might be more efficient to distinguish true epifaunal species. However, the results of this study reveal variations between species MPDs and the distribution of individual abundances along sediment depths.

Assuming that sampling of the sediment with a gravity corer does not drag the sediment down along the tube as the core penetrates the sediment and that individuals do not move after the core penetrates the sediment until the sediments are sub-sampled, all the individuals belonging to an epifaunal species should be found in the top 0.5 cm of sediment. Several factors may explain why this type of a distribution was not found in this study: (1) epifaunal individuals dig in the sediment as the core is sampled; (2) the sediment is disturbed as the core is sampled, and a portion of sediment can be dragged down along the corer; (3) epifaunal species are not ‘true’ epifaunal species and do occasionally dig in the sediment, even if only into the few mm or cm below the sediment–water interface, i.e. ‘true’ epifaunal ostracods do not exist but may be considered as being preferentially epifaunal; and (4) all of the species found during this study are infaunal. Point 1 has already been discussed above and has been considered as having a potential influence on the results found during this study. Point 2 has not been strictly tested, but water–sediment interfaces are always at least slightly disturbed, and the sediment of the upper layer has often been dragged down along the tube. Concerning Point 3, direct observations carried out on *Cypridopsis vidua* in microaquaria have shown that this species, which is commonly considered as epibenthic (and, therefore, also epifaunal), is able to explore the interstices of the sediment (Roca & Danielopol, 1991). These observations suggested that Point 3 may also explain why the maximal relative individual abundance found in the top 0.5 cm of sediment has never been close to 100%. If Point 4 holds true, then it is meaningless to try to determine which species are epifaunal. However, characterising microhabitat preferences in terms of the habitat sediment depth for the species encountered in lake sediments remains an important issue. Regardless, for species being preferentially epifaunal or having shallow sediment depth habitats (e.g. <0.5 cm below the water–sediment

interface), the maximal relative individual abundance must be found in the top 0.5 cm of sediment, whereas for species having deeper habitats (e.g. >0.5 to 1 cm or more, below water–sediment interface), lower abundances must be found within the top 0.5 cm of sediment. Thus, the differences detected between the relative individual abundances in the top 0.5 cm of sediment may also help to distinguish between more surficial and deeper habitats. Because the authors found more than 50% of their populations in the first 0.5 cm of the sediment and a low maximal individual penetration, as presented in Fig. 4, *L. sanctipatricii*, *I. beauchampi*, *C. ophthalmica* at 13 m, *L. inopinata*, and winter *H. reptans* (referred to here as ‘preferentially epifaunal’ populations) seem to favour more surficial habitats compared to all of the other populations. In contrast, *C. neglecta* at 33 and 70 m and summer *H. reptans* present deeper habitats, with less than 10% of their populations being found in the top 0.5 cm of sediment and having high maximal penetration depths. This pattern is supported by the calculated MPDs, as the ‘preferentially epifaunal’ populations have MPDs ranging between 0.45 and 0.81 cm, whereas all of the other populations (referred to here as ‘infaunal’ populations) have MPDs ranging between 0.65 and 1.30. The graph obtained from the PCA (Fig. 3) shows the same pattern, such that ‘preferentially epifaunal’ populations are found on the left upper side of the graph, whereas *C. neglecta* at 33 and 70 m and summer *H. reptans* are found in the right extremity of the scatter plot. According to these results, ‘infaunal’ populations present the deepest habitat preferences, whereas populations belonging to the ‘preferentially epifaunal’ classification present the more surficial habitats. Consequently, we suggest that for the ‘Petit-Lac,’ the ‘preferentially epifaunal’ populations (*L. sanctipatricii*, *I. beauchampi*, *C. ophthalmica* at 13 m, *L. inopinata*, and winter *H. reptans*) may be regarded as being principally epifaunal. In contrast, the other populations can be regarded as infaunal, with different sediment habitat depths according to the species-specific habitat depth preferences (e.g. *C. neglecta* presents a deeper habitat compared with *C. lacustris*) and to the sediment characteristics (e.g. individuals are found deeper in soft sediment compared with more compact sediment).

The relatively deep penetration depth found for *C. ophthalmica* forma *lacustris* at the 70-m water

depth is surprising. At the 13-m water depth, *C. ophthalmica* forma *lacustris* has a surficial habitat. In addition, *C. ophthalmica* (s.str.) is generally described as an epifaunal form and possesses well-developed natatory setae (Meisch, 2000). However, an unusual infaunal microhabitat for *C. ophthalmica* was previously observed in Loch Ness, where the species was homogeneously distributed down to 5 cm within the sediment (Griffiths & Martin, 1993). Still, it is not known if this habitat depth in profundal sites is permanent or, rather, related to a temporary search for food or shelter.

The results of this study indicate that *C. candida* exhibits relatively deep habitats compared with the habitats found for the other species living at the same site. However, these results must be treated with caution because the MPDs, PCA, and cumulative relative individual abundances along the sediment depth profile (Table 5; Figs. 3, 4) were calculated on the basis of only nine and eight individuals for the sites at the 13- and 33-m water depths, respectively, and might, therefore, hint at a more surficial habitat of species at these sites.

Conclusions

The above results from Lake Geneva show that *I. beauchampi*, *L. sanctipatricii*, *L. inopinata*, and the winter generation of *H. reptans* live mostly on, or immediately below the sediment surface (the MPDs for ‘Ad + A-1’ individuals equal 0.45, 0.48, 0.60, and 0.81 cm, respectively) and can be regarded as being principally epifaunal. *Candona neglecta* presents the deepest sediment depth habitats, with MPDs equal to 0.65, 1.22, and 1.33 cm at 13-, 33-, and 70-m water depths, respectively. *Cytherissa lacustris*, the summer generation of *H. reptans*, and *F. caudata* were found at shallower depths in the sediment but are still considered as being infaunal, with MPDs ranging from 0.61 to 1.03 cm. *C. ophthalmica* forma *lacustris* presented two types of microhabitats. At the 13-m water depth, this species can be regarded as being principally epifaunal (MPD = 0.49 cm), whereas this species presents an infaunal habitat at the 70-m water depth (MPD = 0.96 cm). The results for *C. candida* indicate that this species can also be included in the infaunal forms, but these results must

be treated with caution because of the low number of individuals available for calculations.

In addition to species-specific habitat preferences, individual penetration depth increases with developmental stage. In Lake Geneva, the ostracod sediment penetration depth also increases with water depth. This deepening of ostracod habitats has been attributed to a ‘softening’ of sediments as the water depth increases, rather than being due to a variation of the oxygen content in sediment pore water.

Because the micro-environment where ostracods moult is important for making interpretations based on the geochemistry and ecology of ostracods, the results presented here might be relevant to the study of ostracod (palaeo-)ecology in other basins at different geographical and temporal scales.

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