Belg. J. Zool., 143(1) : 42-68 January 2013

Autecology of the extant ostracod fauna of Lake Ohrid and adjacent waters - a key to paleoenvironmental reconstruction

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ABSTRACT. Understanding the ecology of bioindicators such as ostracods is essential in order to reconstruct past environmental and climate change from analysis of fossil assemblages preserved in lake sediment cores. Knowledge of the ecology of ancient Lake Ohrid's ostracod fauna is very limited and open to debate. In advance of the Ohrid ICDP-Drilling project, which has potential to generate high-resolution long-term paleoenvironmental data of global importance in paleoclimate research, we sampled Lake Ohrid and a wide range of habitat types in its surroundings to assess 1) the composition of ostracod assemblages in lakes, springs, streams, and short-lived seasonal water bodies, 2) the geographical distribution of ostracods, and 3) the ecological characteristics of individual ostracod species. In total, 40 species were collected alive, and seven species were preserved as valves and empty carapaces. Of the 40 ostracod species, twelve were endemic to Lake Ohrid. The most common genus in the lake was *Candona*, represented by 13 living species, followed by *Paralimnocythere*, represented by five living species. The most frequent species was *Cypria obliqua*. Species with distinct distributions included *Heterocypris incongruens*, *Candonopsis kingsleii*, and *Cypria lacustris*. The most common species in shallow, flooded areas was *H. incongruens,* and the most prominent species in ditches was *C. kingsleii*. *C. lacustris* was widely distributed in channels, springs, lakes, and rivers. Statistical analyses were performed on a "Lake Ohrid" dataset, comprising the subset of samples from Lake Ohrid alone, and an "entire" dataset comprising all samples collected. The unweighted pair group mean average (UPGMA) clustering was mainly controlled by species-specific depth preferences. Canonical Correspondence Analysis (CCA) with forward selection identified water depth, water temperature, and pH as variables that best explained the ostracod distribution in Lake Ohrid. The lack of significance of conductivity and dissolved oxygen in CCA of Ohrid data highlight the uniformity across the lake of the well-mixed waters. In the entire area, CCA revealed that ostracod distribution was best explained by water depth, salinity, conductivity, pH, and dissolved oxygen. Salinity was probably selected by CCA due to the presence of *Eucypris virens* and *Bradleystrandesia reticulata* in short-lived seasonal water bodies. Water depth is an important, although indirect, influence on ostracod species distribution, which is probably associated with other factors such as sediment texture and food supply. Some species appeared to be indicators for multiple environmental variables, such as lake level and water temperature.

KEY WORDS: freshwater Ostracoda, endemism, ancient lakes, multivariate analysis, training set

INTRODUCTION

Ostracods (Arthropoda) are bivalved crustaceans with adults being typically 0.5 to 3.0mm long. They are environmentally and geographically diverse, and are often abundant in almost all aquatic and in some terrestrial habitats (De Deckker & Forester, 1988; Holmes, 2001; Smith & Delorme, 2009). In common with diatoms, cladocerans, and thecamoebians, for example, ostracods are one of the few aquatic organisms that can be recovered as fossils in statistically relevant numbers. They are strong tools for paleoecological interpretations because of their excellent shell preservation, their small size, diversity, and sensitivity to a wide range of environmental variables (Delorme, 1969). Traditionally, most ostracod specialists have focused more on taxonomic problems than on defining ecological response. For robust paleoenvironmental interpretation of preserved fossil ostracod records, a sound knowledge of ostracod ecology is vital (De Deckker & Forester, 1988). Important environmental variables determining the presence and distribution of ostracod species can be divided into habitat characteristics and the nature of the host water. The former includes the size, energy level, permanence of the water body, water depth, sediment texture, presence and types of aquatic plants, availability of food, and predation. The latter comprises nutrient status, pH, dissolved oxygen content, salinity, temperature, and ionic composition of the host water (Holmes, 2001). Besides their potential as a tool for paleoecological reconstruction, they can also be used as indicators of ecosystem health. For example, Külköylüoglu (2004) suggested that ostracods are excellent water quality indicators. Similarly, Pieri et al. (2012) investigated the impact of wastewater discharge on ostracod density, richness, and community composition, highlighting their value as water quality indicators. Transfer functions are a common approach to reconstruct past environments. Reed et al. (2008) applied a diatom-inferred total phosphorus transfer function to demonstrate that Lake Uluabat (Turkey) has been eutrophic since prior to the 19th century. Mezquita et al. (2005) found that ostracods from the eastern Iberian Peninsula have potential both for reconstructing past water temperatures and water chemistry (solute concentration and composition). However, transfer functions are not infallible. Sometimes, due to the nature of variation in the calibration dataset, ecologically insignificant variables may appear to exert a significant influence on species distribution. To minimize this risk, care must be taken to ensure that both the training set and the variation in the environmental variable of interest are sufficiently large (Telford & Birks, 2011a, b).

In Lake Ohrid, the pioneering investigation of the ostracod fauna in 1934 (Klie, 1934) was soon followed by a series of others (Holmes, 1937; Klie, 1939a, b, 1942; Petkovski, 1960a, b, c; Mikulić, 1961; Petkovski, 1969a, b; Mikulić & Pljakić, 1970). These studies focused on acquisition of the species inventory and taxonomy. Except for some information on species sampling depth, knowledge on the autecology of the predominantly endemic ostracods from Lake Ohrid and its surroundings is lacking (Belmecheri et al., 2009; Aufgebauer et al., 2012). This study aims to define baseline ecological information to contribute to future studies on the long sequence obtained during the ICDP-Drilling in Lake Ohrid in 2013. In parallel, it aims to generate information on the indicator value of individual ostracod species for water quality assessment, which could be used to tackle the “creeping biodiversity crisis” in this World Heritage Site (Kostoski et al., 2010). To achieve this goal, we collected surface sediments and water samples from different habitat types, e.g., Lakes Ohrid, Prespa, Dojran, and Ioannina as well as short-lived seasonal water bodies, springs, and streams, and compiled a detailed species inventory. To attempt to define species-specific environmental preferences, optimum values and tolerance ranges were estimated using the transfer function approach (Smol, 2002). Furthermore, the geographical distribution of the ostracod species in the region was determined.

MATERIALS AND METHODS

Study area

Situated in the southern Balkans (Fig. 1), the study area is located in a highly diverse biogeographic region, characterized by a large number of ancient lakes including Lakes Ohrid, Prespa, Dojran, and Ioannina (Griffiths et al., 2002b; Frogley & Preece, 2004; Reed et al., 2004; Albrecht et al., 2009) which are a focus for the current study. The region is relatively arid, with fewer lakes than, for example, northwestern Europe. Lakes Ohrid and Prespa are both deep and relatively low in nutrients, whereas Lakes Dojran and Ioannina are shallow and currently hypereutrophic. The oligotrophic, karstic Lake Ohrid lies on the border between Macedonia and Albania at 695m a.s.l. It has a surface area of 358km^2 and a maximum depth of 288.7m. Lake

Ohrid is directly connected with Lake Prespa via underground karstic channels (SALEMAA, 1994; ALBRECHT & WILKE, 2008). Both lakes are Quaternary graben-shaped lakes formed by a combination of post-Pliocene uplift and gradual subsidence (ALIAJ et al., 2001). Lake Prespa, with a surface area of 254km^2, is situated on the Macedonian-Albanian-Greek border at an altitude of 849m. Its maximum water depth is 48m, having undergone a ca. 6m reduction in lake level since the 1950s due to increasing water abstraction for irrigation. The lake may also be suffering from anthropogenic eutrophication (LÖFFLER et al., 1998; MATZINGER et al., 2006). Lake Dojran (146-148m a.s.l.) lies between the borders of Macedonia and Greece in a karstified basin formed by Tertiary volcanic and tectonic activity. The maximum surface area is approximately 40km^2, the maximum depth was 10.4m in the 1930s but by 1995 had fallen by 4.8m due to water abstraction (GRIFFITHS et al., 2002a). The southernmost study site is Lake Ioannina (also known as Lake Pamvotis), located in northwest Greece at 480m a.s.l. in a karst polje, a depression, formed during the Late Pliocene to Early Pleistocene. The catchment consists mainly of Mesozoic and early Cenozoic limestone bedrock overlain by thick deposits of Late Pliocene and Quaternary lake sediments. The lake level of Lake Ioannina also dropped markedly during the first half of the twentieth century as a result of agricultural drainage. The modern lake is a remnant of the ancient lake, with a surface area of ca. 23km^2 and a maximum water depth of 10m (FROGLEY et al., 2001; LENG et al., 2010).

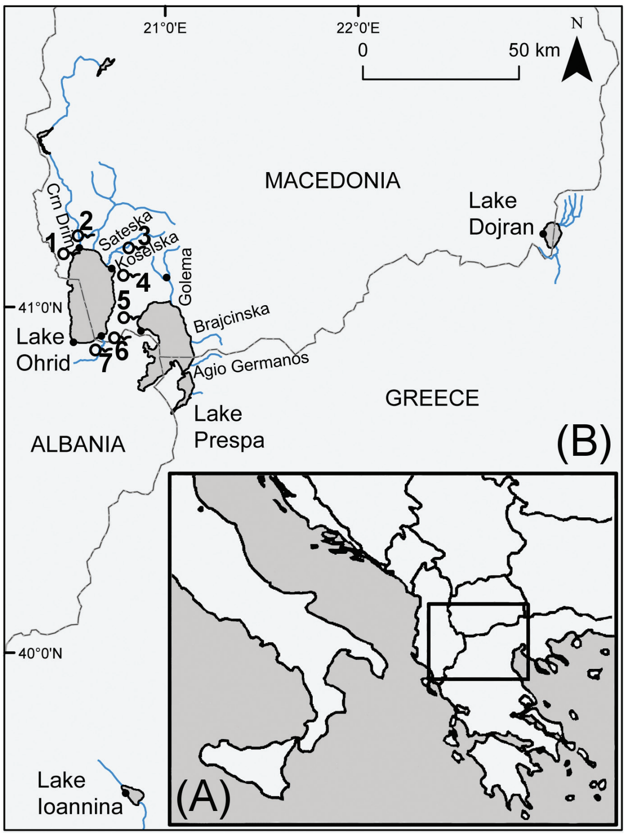

Fig. 1. – Map showing the location of the study area (marked with a square) in Macedonia, Albania, and Greece (A) and basic hydrological features (B). Numbers indicate major sampled springs (1: Kališta springs, 2: Šum springs, 3: Bej wells, 4: Biljana springs, 5: Korita springs. 6: Sveti Naum, 7: Tushemisht springs).

The watersheds of Lakes Prespa and Ohrid are estimated to be 1391km^2 and 1002km^2, respectively. Because of the irregular and strongly developed surface terrain morphology partly underlain by deep karst it is difficult to define the exact watershed and catchment areas. Numerous karst springs occur within Lake Ohrid and at the lakeshore (POPOVSKA & BONACCI, 2007). At Sveti Naum, on the southeastern shore of Lake Ohrid, eight springs form a small pond, which collects the spring waters before draining into Lake Ohrid (JORDANOSKA et al., 2010). The Tushemisht spring zone, west of Sveti Naum, in Albania, consists of 80 individual springs. Other springs are the Biljana, at the Hydrobiological Institute in the City of Ohrid, and the Bej wells which are located northeast of Lake Ohrid (POPOVSKA & BONACCI, 2007). The Kališta springs are located at the northwestern shore of the lake, the Šum springs north of Lake Ohrid, and the Korita springs between Lake Ohrid and Lake Prespa (Fig. 1).

Lakes Ohrid and Prespa are influenced by a continental climate. For the period 1961-1990 the average annual air temperature was 11.1°C in the City of Ohrid. The minimum air temperature was -5.7°C and the maximum 31.5°C. In Resen, 10km north of Lake Prespa, average annual air temperature of 9.5°C was registered. The minimum air temperature was -8.7°C and the maximum air temperature 30.5°C (Popovska & Bonacci, 2007). Maximum precipitation occurs in December and March, whereas the late summer is dry. In summer, the winds are predominantly southwestern (Salemaa, 1994). Lake Dojran has a Mediterranean climate with an average annual precipitation of 623.4mm (average for the period 1961-1990) (Popovska & Bonacci, 2008) in Nov Dojran, west of the lake. The summers are long and hot, and the winters are mild. Highest average long-term monthly temperatures occur in July and August (19.1°C and 18.7°C) and lowest temperatures in January and February (0.6°C and 1.9°C) (Popovska & Bonacci, 2008). Lake Ioannina is influenced by a semi-humid Mediterranean climate. The winters are cold and wet with a mean temperature in January of 4.9°C. Summers are hot and dry, with a mean temperature in July of 24.9°C. The mean annual temperature is 14.4°C, and the annual precipitation is approximately 1100-1200mm (Tzedakis, 2000; Romero et al., 2002).

Field and laboratory analysis

A total of 335 surface sediment samples were collected during four field campaigns in March/April 2009, August/September 2009, February 2010, and June 2010 in Lake Ohrid (Macedonia, Albania) and its surrounding areas including Lakes Prespa (Macedonia, Albania, Greece) and Ioannina (Greece) as well as from springs, rivers, flooded areas, ditches, and channels. Samples taken in September 2009 from Lake Dojran (Macedonia, Greece) were provided by Thomas Wilke and his team, Justus-Liebig-Universität Gießen, Germany. Deeper parts of Lake Ohrid (from 5 to 280m water depths) were sampled with a gravity multicorer, consisting of three cores with a diameter of 11cm each, and short core tops (uppermost 2cm≙190cm^3) were used for ostracod analysis. In shallower waters and in places where sediments were stony, it was impossible to use the multicorer. There, samples were retrieved with either an exhauster, spoon net, UWITEC-gravity corer, Ekman grab (uppermost 2cm), dredge or with a sediment suction device. This device is composed of a manual membrane pump with a flexible hose of 5m length to which a metal pipe is attached allowing for sampling between rocks and stones. All samples were washed through a 125µm mesh sieve immediately after collection and were preserved in 95-99% ethanol. *In situ*, dissolved oxygen, pH, conductivity, salinity, and water temperature were measured with a handheld multi-sensor (Multi 3500i Hand-Held Meter, WTW) and water transparency with a Secchi disc. A WinLab Data Line Photometer (Windaus) was used to analyze nutrients and major ions including sulfate, phosphate, ammonium, nitrite, and nitrate. Water samples were collected for the additional measurement of major and trace elements. Lake waters from deeper sites (>5m) were obtained either with a Niskin Type water sampler, or bottom water trapped above core tops during collection of short cores was used. Substrate was described in the field and classified into detritus, sapropel, artificial, rocks (>200mm), stones (200-63mm), gravel (63-2mm), sand (2-0.063mm), and silt/clay (<0.063mm). Water chemistry was analyzed at the Technische Universität Braunschweig, Germany, using Ion Chromatography with a 761 Compact IC Metrohm and Inductively Coupled Plasma Optical Emission with an ICP-OES Jobin Yvon JY 50 P, and at the Freie Universität Berlin, Germany, using a DIONEX DX-500 Ion Chromatograph, ICP-OES Perkin Elmer Optima 2100DV, and Technicon DOC-Auto-Analyzer II. Surface sediment samples were hand-sorted under a dissecting microscope with a magnification up to 50x. The preparation of soft parts used for identification of species was carried out using traditional embedding in Hydro-Matrix™ (Micro Tech Lab). Scanning Electron Microscope (SEM) pictures of ostracod valves were taken at the Zoological Museum of the Universität Hamburg with a Scanning electron microscope LEO 1525 (Carl Zeiss Inc.), and at the Universität Köln with a CamScan-CS-44 (CamScan). Digital images were taken with a light microscope (DM5000B; camera type Leica DFC320), and single pictures were stacked with the software package CombineZ. Ostracod identification was based on taxonomic work by Klie (1934, 1939a, b, 1942), Petkovski (1960a, b, c), Mikulić (1961), Petkovski (1969a, b), Meisch (2000), and Petkovski et al. (2002).

Data analysis

Quantitative data analysis was based on adults of living ostracods. Indeterminate juveniles, empty carapaces and valves were omitted because they may have been transported by drift, particularly in shallow depths and on rocky substrates, and thus do not necessarily present the true species assemblage (Park et al., 2003). Analyses are based on relative abundances, because this is more robust. In total 74 samples did not contain ostracods and were therefore excluded from analysis; the dataset therefore comprises 211 samples. Secchi depth was also excluded from statistical analyses as the Secchi disk was in most cases visible all the way down to the bottom of the aquatic habitat (<20m) and Secchi depth therefore corresponds to water depth. Pearson correlation, cluster analysis, and ordinations were performed with two different datasets to determine whether ostracod species in Lake Ohrid were affected by other environmental variables than those found over the full sample area. The entire dataset consisted of all sampled habitats, whereas the Lake-Ohrid dataset included only the samples from Lake Ohrid.

The unweighted pair group mean average (UPGMA) with Jaccard's coefficient was used to show a possible clustering relationship among ostracods; it was performed with the program MVSP (MultiVariate Statistical Package), version 3.21. The program Past, version 2.12 (Hammer et al., 2001) was used for SIMPER (Similarity percentage) to assess ostracod species that accounted for the greatest observed differences in ostracod composition between various habitats, and for Pearson correlations, to assess relationships between the environmental variables. Distribution maps of ostracod species were created in ESRI Arc Map 9.3. Grapher version 9.1.536 was used to prepare pie charts illustrating the link between grain size and ostracod distribution.

Detrended Correspondence Analysis (DCA) (Hill & Gauch, 1980), with detrending by segments and non-linear rescaling, was used to decide whether unimodal (gradient length >2 SD (standard deviation units)) or linear (gradient length <2 SD) based numerical techniques should be used (Smol, 2002). Because DCA revealed gradient lengths of 4.71 (first axis) and 3.77 SD (second axis) for the entire dataset, as well as 4.82 (first axis) and 4.38 SD (second axis) for the Lake-Ohrid dataset, we used Canonical Correspondence Analysis (CCA) (ter Braak, 1986) to explain the relationships between ostracod species and their environment. For CCA analysis, rare species were down-weighted, ostracod data were log-transformed, and environmental variables were added by manual forward selection using the Monte Carlo permutation test with 999 permutations. All ordinations were performed using Canoco version 4.5 (ter Braak & Smilauer, 2002), and ordination diagrams were made with CanoDraw 4.0. Weighted averaging (WA) regression with inverse deshrinking was used to calculate the ecological tolerance range and the optima of the most common ostracod species. This was performed with the program C2 version 1.7.2 (Juggins, 2007) for significant environmental variables only ($P<0.05$). The 16 rare species, present in ≤3 waterbodies each, were excluded from UPGMA clustering, DCA, CCA, and WA to avoid distortion.

RESULTS

Habitat preferences

A total of 47 ostracod species was found, belonging to 18 genera (Table 1, Figs 1S-3S, supplementary material). Forty species were collected alive, and seven species were identified using valves or empty carapaces only. The soft parts of the ostracods were used for preliminary species identification and a detailed description

TABLE 1

Taxonomic ranking of ostracod species (species marked with asterisks (*) were identified using valves or empty carapaces). Abbreviations of each taxon (used in subsequent tables and figures) are indicated after their respective names.

Class Ostracoda Latreille, 1806	
Order Podocopida Sars, 1866	
Suborder Podocopina Sars, 1866	
Infraorder Cypridocopina Jones, 1901	
Superfamily Cypridoidea Baird, 1845	
Family Candonidae Kaufmann, 1900	
Subfamily Candoninae Kaufmann, 1900	
Genus *Candona* s. str. Baird, 1845	
Candona bimucronata Klie, 1937	Cbimu
**Candona expansa* Mikulić, 1961	
Candona goricensis Mikulić, 1961	Cgori
Candona hadzistei Petkovski et al., 2002	Chadz
Candona hartmanni Petkovski, 1969	Chart
**Candona holmesi* Petkovski, 1960	
Candona litoralis Mikulić, 1961	Clito
Candona margaritana Mikulić, 1961	Cmarga
**Candona marginata* Klie, 1942	
Candona marginatoides Petkovski, 1960	Cmargi
Candona media Klie, 1939	Cmedi
Candona ohrida Holmes, 1937	Cohri
Candona ovalis Mikulić, 1961	Coval
Candona trapeziformis Klie, 1939	Ctrap
**Candona triangulata* Klie, 1939	
Candona vidua Klie, 1941	Cvidu
Genus *Fabaeformiscandona* Krstić, 1972	
Fabaeformiscandona krstici Petkovski, 1969	Fkrst
Genus *Pseudocandona* Kaufmann, 1900	
Pseudocandona compressa (Koch, 1838)	Pcomp
Genus *Candonopsis* Vávra, 1891	
Candonopsis kingsleii (Brady & Robertson, 1870)	Cking
Subfamily Cyclocypridinae Kaufmann, 1900	
Genus *Cypria* Zenker, 1854	
Cypria lacustris Sars, 1890	Cypla
Cypria obliqua Klie, 1939	Cyobl
**Cypria ophtalmica* (Jurine, 1820)	
Genus *Cyclocypris* Brady & Norman, 1889	
Cyclocypris ovum Jurine, 1820	Covum
Family Ilyocyprididae Kaufmann, 1900	
Subfamily Ilyocypridinae Kaufmann, 1900	
Genus *Ilyocypris* Brady & Norman, 1889	
Ilyocypris bradyi Sars, 1890	Ibrad
Family Cyprididae Baird, 1845	
Subfamily Eucypridinae Bronshtein, 1947	
Genus *Eucypris* Vávra, 1891	
Eucypris virens (Jurine, 1820)	Evire

Eucypris sp.	Esp
Genus *Prionocypris* Brady & Norman, 1896	
Prionocypris zenkeri (Chyzer & Toth, 1858)	Pzenk
Subfamily Cypricercinae McKenzie, 1971	
Genus *Bradleystrandesia* Broodbakker, 1983	
Bradleystrandesia reticulata (Zaddach, 1844)	Breti
Subfamily Herpetocypridinae Kaufmann, 1900	
Genus *Herpetocypris* Brady & Norman, 1889	
Herpetocypris sp.	Hsp
Herpetocypris sp. 2	Hsp2
Genus *Psychrodromus* Danielopol & McKenzie, 1977	
Psychrodromus fontinalis (Wolf, 1920)	Pfont
Psychrodromus olivaceus (Brady & Norman, 1889)	Poliv
Psychrodromus sp.	Psp
Subfamily Cyprinotinae Bronshtein, 1947	
Genus *Heterocypris* Claus, 1892	
Heterocypris incongruens (Ramdohr, 1808)	Hinco
Heterocypris reptans (Baird, 1835)	Hrept
**Heterocypris salina* (Brady, 1868)	
Subfamily Dolerocypridinae Triebel, 1961	
Genus *Dolerocypris* Kaufmann, 1900	
Dolerocypris sinensis (Sars, 1903)	Dsine
Superfamily Cytheroidea Baird, 1850	
Family Leptocytheridae Hanai, 1957	
Subfamily Leptocytherinae Hanai, 1957	
Genus *Amnicythere* Devoto, 1965	
Amnicythere karamani (Klie, 1939)	Akara
Family Limnocytheridae Klie, 1938	
Subfamily Limnocytherinae Klie, 1938	
Genus *Paralimnocythere* Carbonnel, 1965	
Paralimnocythere alata (Klie, 1939)	Palat
Paralimnocythere georgevitschi (Petkovski, 1960)	Pgeor
Paralimnocythere karamani (Petkovski, 1960)	Pkara
Paralimnocythere ochridense (Klie, 1934)	Pochr
Paralimnocythere slavei Petkovski, 1969	Pslav
**Paralimnocythere umbonata* (Klie, 1939)	
Subfamily Timiriaseviinae Mandelstam, 1960	
Genus *Kovalevskiella* Klein, 1963	
Kovalevskiella sp.	Ksp
Family Cytherideidae Sars, 1925	
Genus *Cytherissa* Sars, 1925	
Cytherissa lacustris (Sars, 1863)	Cytla
Infraorder Darwinulocopina Sohn, 1988	
Superfamily Darwinuloidea Brady & Norman, 1889	
Family Darwinulidae Brady & Norman, 1889	
Genus *Darwinula* Brady & Robertson, 1885	
Darwinula stevensoni (Brady & Robertson, 1870)	Dstev

and documentation of the Ohrid ostracod soft part morphology is planned for the near future (Lorenschat et al., in preparation). In certain cases, it is possible to determine ostracods to the species level on valve morphology alone. For example, the valves of *Amnicythere karamani* (Klie, 1939) are, in contrast to other *Amnicythere* species in the western Balkan Peninsula, covered with coarse pits (Petkovski & Keyser, 1992), while the valves of the species of *Paralimnocythere* have a specific number and typical array of prominent ridges, tubercles, and ala (lateral projections) (Meisch, 2000). Distinctive features of *Candona* species are the valve size and the valve outlines, as described in the literature, e.g., Mikulić (1961).

Thirty-two out of the 40 living ostracod species occurred in Lake Ohrid, and twelve were discovered exclusively in the lake (Fig. 4S, supplementary material). Furthermore, valves and empty carapaces of *Candona expansa* Mikulić, 1961, *Candona holmesi* Petkovski, 1960, *Candona marginata* Klie, 1942, *Candona triangulata* Klie, 1939, and *Cypria ophtalmica* (Jurine, 1820) were found in Lake Ohrid. Empty carapaces of *Paralimnocythere umbonata* (Klie, 1939) occurred in one sample from the springs of Sveti Naum and in Lake Ohrid. In the littoral zone of Lake Dojran, living specimens of *Cypria lacustris* Sars, 1890 and *Herpetocypris* sp. as well as valves and empty carapaces of *Heterocypris salina* (Brady, 1868) were collected. The littoral of Lake Prespa was inhabited by *Candona marginatoides* Petkovski, 1960, *Cyclocypris ovum* Jurine, 1820, *Cypria lacustris*, *Darwinula stevensoni* (Brady & Robertson, 1870), *A. karamani*, *Paralimnocythere ochridense* (Klie, 1934), and *Bradleystrandesia reticulata* (Zaddach, 1844). *Candona media* Klie, 1939 and *D. stevensoni* were the only species that were recovered alive in the littoral of Lake Ioannina. The most common genus in the study area was *Candona,* represented by a total of 13 living species, followed by *Paralimnocythere* with five living species. The most common species was *Cypria obliqua* Klie, 1939 which was found in 120 samples (36%) (Fig. 4S, supplementary material). Other common species were *C. media* (in 76 samples), *Cypria lacustris* (in 70 samples), and *A. karamani* (in 60 samples). Furthermore, most of the sampled habitats were inhabited by a large number of juvenile ostracods of the genera *Candona* and *Cyclocypris* that were indeterminable to species level. For instance, in a sample taken with the suction device at 0.5m water depth on the eastern shore of the lake, a total of 1432 ostracod specimens was found, of which 1358 were juvenile Candonids. The 74 samples devoid of ostracods were mainly those of rivers and streams with a strong water current and a substrate mainly consisting of rocks, stones, and gravel. Samples from the littoral of Lake Ohrid, where coarse material (rocks, stones, and gravel) predominated, and wave action was strong, were also devoid of ostracods. The deepest sample from Lake Ohrid that did not contain ostracods was taken in 20m water depth at the eastern shore (coarse material and steeply sloping shore). All the other sampled localities from deeper waters in Lake Ohrid were inhabited by ostracods.

Relative abundance species data from the entire dataset, consisting of 211 surface sediment samples, clustered into six main groups (Fig. 5S, supplementary material). Group 1 contained only the species *Heterocypris incongruens* (Ramdohr, 1808). This was the only species found in the surrounding areas of Lake Ohrid, not in the lake itself; and it always occurred in very shallow water (maximum sampling depth 0.3m). The only species in Cluster Group 2 was *Paralimnocythere karamani* (Petkovski, 1960). It was only discovered at three localities in Lake Ohrid and in Sveti Naum, in shallow waters from 0.2m down to 54m depth and at low water temperatures (<11.5°C). Five species (*Ilyocypris bradyi* Sars, 1890, *Cytherissa lacustris* (Sars, 1863), *B. reticulata*, *Eucypris virens* (Jurine, 1820), and *Candona hartmanni* Petkovski, 1969) were found in Cluster Group 3. All species in this group inhabited water depths from 0.5m down to 40m, and waters with temperatures between 17°C and 23°C. Group 3 can be divided into four subgroups (a, b, c, and d) (Fig. 5S, supplementary material). The most common species was *C.*

hartmanni (subgroup d) with six occurrences in Lake Ohrid and two occurrences in springs (Sveti Naum and Bej wells). *B. reticulata* and *E. virens* (subgroup c) were species associated to waters with a very high conductivity. *Candona litoralis* Mikulić, 1961 (cluster group 4) was the only species in Lake Ohrid restricted to the shallower littoral (maximum sampling depth 5m). *Candona hadzistei* Petkovski et al., 2002, *Fabaeformiscandona krstici* Petkovski, 1969, *C. marginatoides*, *C. media*, *Candona ovalis* Mikulić, 1961, *Candona vidua* Klie, 1941, *C. obliqua*, *A. karamani*, and *Candona trapeziformis* Klie, 1939 clustered in Group 5. *C. trapeziformis* inhabited Lake Ohrid down to 163m depth and all the other species occurred down to 280m water depth. Cluster Group 6 included *C. ovum*, *Cypria lacustris*, *P. ochridense*, *Paralimnocythere slavei* Petkovski, 1969, *Candona ohrida* Holmes, 1937, *Candonopsis kingsleii* (Brady & Robertson, 1870), and *D. stevensoni*. They colonized different water depths but were more common at lower depths (1.7-19.5m). Furthermore, all species were found in waters with a maximum temperature of 26°C.

For the Lake Ohrid dataset, consisting of 160 surface sediment samples, the UPGMA dendrogram revealed three major clustering groups (Fig. 6S, supplementary material). Group 1 included *C. litoralis* and *C. hartmanni*. These species were restricted to 5m and 10m water depth, respectively. Cluster Groups 2 and 3 of the Lake-Ohrid dataset were similar to Cluster Groups 5 and 6 from the entire dataset.

Ostracods occurred in almost all aquatic habitats. Species-specific environmental preferences were suggested by the SIMPER output (Table 1S, supplementary material). All lakes, except for Lake Ohrid, were considered as an individual group because samples were taken only in the littoral zone, so that these do not reflect the complete ostracod fauna of the lakes (e.g., species that inhabit only deeper parts of the lakes were not found). SIMPER indicated that the maximum average dissimilarity between the habitats was 99.96% (flooded areas and rivers), and the minimum 38.05% (channels and lake habitats). SIMPER results also define characteristic indicator species for specific habitats: *H. incongruens* for flooded areas, *C. kingsleii* for ditches, *C. obliqua* for Lake Ohrid, and *Cypria lacustris* for channels, springs, lakes, and rivers.

Candona margaritana Mikulić, 1961, *Kovalevskiella* sp., and *P. karamani* were restricted to sediments with a minimum of 50% sand content (Fig. 7S, supplementary material). Six species (*Candona bimucronata* Klie, 1937, *C. litoralis*, *C. ohrida*, *C. kingsleii*, *D. stevensoni*, and *P. slavei*) were found on substratum that consisted of at least 50% of coarse sediment (rocks, stones, and gravel), and 16 species preferred mainly silty sediment.

Response to limnological variables

Correlations between the variables (Table 2S and Table 3S, supplementary material) were similar in both datasets, with few significant correlations. The only noticeable difference was the high correlation between NO_2 and NH_4 (0.84) in the entire dataset compared to 0.47 in Lake Ohrid dataset.

The first CCA focused on the entire dataset and the first two axes of the DCA explained 20.9% of the variability in species data. The sum of all canonical eigenvalues was 0.91. The first two axes of the CCA explained 6.5% (Table 2) of the variance in the species data. Water depth, salinity, conductivity, pH, and dissolved oxygen were identified by forward selection as variables that best explained the variation in ostracod species data (Table 3). The first synthetic gradient was positively correlated with salinity and conductivity and negatively with water depth, pH, and dissolved oxygen (Fig. 2). Furthermore, dissolved oxygen and pH were negatively correlated with the second axis, and conductivity, salinity, and water depth were positively correlated with the second axis. All species located with negative axis 2 scores, were found in water depths down to 280m, except for

TABLE 2

Summary of results from CCA performed on the entire dataset.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.34	0.14	0.11	0.08	7.27
Species-environment correlation	0.73	0.55	0.46	0.47	
Cumulative percentage variance					
of species data	4.70	6.50	8.00	9.10	
of species-environment relation	37.30	52.00	63.80	72.50	
Sum of all eigenvalues					7.27
Sum of all canonical eigenvalues					0.91

C. trapeziformis which occurred in a maximum water depth of 163m. *B. reticulata* and *E. virens* are located in the upper right quadrant of the biplot and were sampled in habitats with high conductivity (Fig. 2). In the majority of cases, the most common ostracod species are grouped in the center of the ordination biplot, for example, *Cypria lacustris,* underlining their apparently broad tolerance ranges.

The second CCA focused on the Lake Ohrid dataset only. In the initial DCA, the first and second axes together explained 23.2% of the variance in species data; the sum of all canonical

TABLE 3

Results of forward selection of explanatory variables (*P*-values ($P<0.05$) and total percent variance explained by each environmental variable) for the entire dataset.

Variable	*P*-value	% total variance explained
Water depth	0.001	22
Salinity	0.003	12
Conductivity	0.007	8
pH	0.003	11
Dissolved oxygen	0.050	5

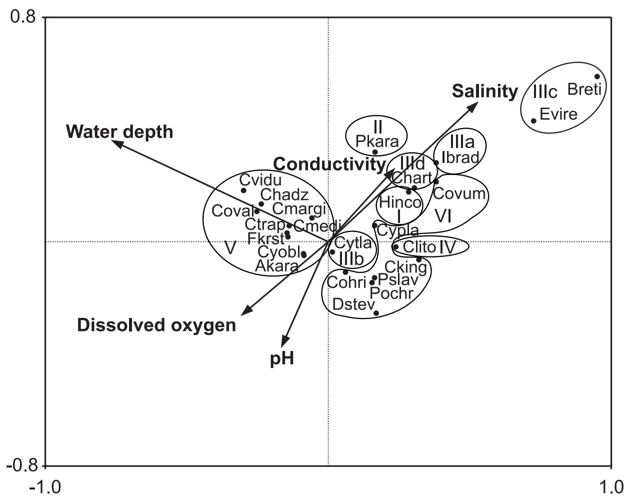

Fig. 2. – Canonical Correspondence Analysis (CCA) biplot of ostracod species and forward selected environmental variables from 211 surface sediment samples taken in Lake Ohrid and its surroundings. Species codes as in Table 1 and roman numerals and characters indicate species assemblages.

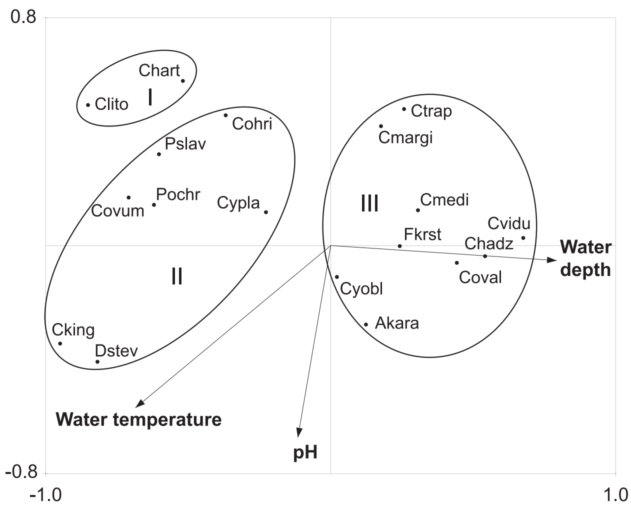

Fig. 3. – Canonical Correspondence Analysis (CCA) biplot of ostracod species and forward selected environmental variables from 160 surface sediment samples taken in Lake Ohrid. Species codes as in Table 1 and roman numerals indicate species assemblages.

TABLE 4

Summary of results from CCA performed on the Lake-Ohrid dataset.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.25	0.09	0.07	0.05	4.14
Species-environment correlation	0.73	0.56	0.48	0.50	
Cumulative percentage variance					
of species data	6.10	8.40	10.00	11.30	
of species-environment relation	40.50	55.50	66.40	75.00	
Sum of all eigenvalues					4.14
Sum of all canonical eigenvalues					0.63

eigenvalues was 0.63. The first two axes of the CCA together explained 8.4% of the variance in the species data (Table 4). Water depth, water temperature, and pH were identified by forward selection as variables that best explain the species distribution (Table 5). The first axis was positively correlated with water depth and negatively with water temperature, and the second axis was strongly negatively correlated with pH (Fig. 3). Species related to deeper waters were located on the upper right side of the biplot. *C. obliqua* was the most common species in Lake Ohrid, and is located in the centre of the biplot.

As indicated by SIMPER, some species occurred in specific habitats and others in a wide range of different environments. Whereas the latter species have a wide tolerance range for particular environmental variables, the former species have a narrow distribution range and are less tolerant. All estimated optima, tolerance ranges, and standard errors for the significant variables and for all species are listed in Table 4S, supplementary material. Nine ostracod species

TABLE 5

Results of forward selection of explanatory variables (*P*-values ($P<0.05$) and total percent variance explained by each environmental variable) for the Lake-Ohrid dataset.

Variable	*P*-value	% total variance explained
Water depth	0.001	17
Water temperature	0.001	9
pH	0.017	5

occurred in Lake Ohrid down to 280m water depth: *C. hadzistei*, *F. krstici*, *C. marginatoides*, *C. media*, *C. ovalis*, *C. vidua*, *C. obliqua*, *Cypria lacustris*, and *A. karamani*. Eight out of these nine species have a high tolerance for water depth (72.3-97.3m); only *Cypria lacustris* showed a lower tolerance range (49.9m) and optimum (19.5m) for depth. *B. reticulata*, *C. hartmanni*, *C. kingsleii*, *C. litoralis*, *E. virens*, and *H. incongruens* occurred in all sampled habitats down to 10 m water depth and all of them have relatively low tolerance ranges (<3.0m) and optimum values (<1.7m). *C. trapeziformis* was the species that always occurred at low water temperatures (< 9.9°C). This species showed the lowest optimum (8.2°C) and a low tolerance range (0.7°C). *H. incongruens* was the species that thrived at highest temperatures (maximum: 33.8°C); it has a high optimum (32.8°C), and a high tolerance range (16.1°C).

DISCUSSION

Understanding the autecology of single ostracod species is important for interpreting past climate and environmental changes. This study provides the first information about the autecology of ostracod species mostly endemic to Lake Ohrid and its surroundings. A total of 40 living ostracod species were found in 335 surface sediment samples from Lake Ohrid and its surroundings of which 32 occurred in the lake itself and twelve species were exclusively found in Lake Ohrid. We collected seven ostracod species in Lake Prespa and, except for *B. reticulata*, all other species were also found by PETKOVSKI (1960b). The two living species, *Herpetocypris* sp. and *Cypria lacustris* sampled in the littoral of Lake Dojran, were not found by GRIFFITHS et al. (2002a). In the littoral of Lake Ioannina, we only found two living species, *C. media* and *D. stevensoni*; only the latter had been recorded there before (FROGLEY et al., 2001).

Cluster analysis and CCA were used to identify the relationship between environmental variables and ostracod distribution. In the UPGMA dendrogram rare species were usually clustered in small groups as is the case in Groups 1-4 of the entire dataset (Fig. 5S, supplementary material), and in Group 1 of the Ohrid dataset (Fig. 6S, supplementary material). Clustering of both datasets was mainly affected by water depth and forward selection of CCA identified water depth, salinity, conductivity, pH, and dissolved oxygen as variables that determine the ostracod distribution in the entire study area. Salinity was probably forward selected because of the presence of species such as *E. virens* and *B. reticulata*, mostly found in waters with the highest salinity (0.1‰). The biplot (Fig. 2) indicated the same ostracod assemblages that were visible in the UPGMA cluster (Fig. 5S, supplementary material). For the Lake Ohrid dataset, water depth, water temperature, and pH were identified as variables that best explained the species distribution within the lake. Probably due to the uniformity of conductivity and dissolved oxygen within the lake, these two variables were not identified as major environmental variables determining ostracod distribution. They did, however, play a major role in determining the distribution of ostracods in the Lake Ohrid surroundings. Strikingly, the "Ohrid-biplot" (Fig. 3) revealed the same groups as the UPGMA cluster (Fig. 6S, supplementary material). Cluster analysis as well as CCA for both datasets revealed water depth as the variable with the strongest apparent influence on ostracod species distribution; while some species that occurred in Lake Ohrid at all depths down to 280m had a relatively broad tolerance to depth, those species that only colonized waters down to 10m depth (*B. reticulata*, *C. hartmanni*, *C. kingsleii*, *C. litoralis*, *E. virens*, and *H. incongruens*) had low tolerances, thus representing excellent indicator species. The results of our CCA analyses agree with several other studies (e.g., BUNBURY & GAJEWSKI, 2005) confirming that water depth is an influential factor affecting ostracod species distribution. As a note of caution, NEALE (1964) has previously argued that the direct influence of water depth *per se* is probably modest. Its apparent influence probably results from a combination of other environmental variables that are closely linked to water depth, such as water temperature, light intensity and hence photosynthesis; these in turn affect both food supply and shelter (NEALE, 1964). It is difficult to identify which variable is linked to water depth in Lake Ohrid, and the Pearson correlations provide no clear evidence. In the entire dataset (Table 2S, supplementary material) water depth showed no correlation and therefore no relationship to any environmental variable. In the Lake Ohrid dataset (Table 3S, supplementary material) water depth is strongly positively correlated to silt (0.83) but otherwise all the other variables are not associated to water depth. This might indicate that the distribution of ostracod species in Lake Ohrid is determined in part by the availability of silt, linked, for example, to food availability. Another factor, which was not observed by us in the field but which may control ostracod distribution is wave energy (MISCHKE et al., 2010) and concomitant sediment disturbance and stability of the environment. Water depth, however, is an important variable in paleoenvironmental reconstructions (MISCHKE et al., 2010) because it provides information about hydrological changes of a lake system that may have been caused by climate change; on the assumption that these relationships are maintained over time, we have a potential tool to reconstruct fluctuations in water depth.

Water temperature also plays an important role in controlling ostracod distribution (e.g., NEALE, 1964; HORNE, 2007; VAN DER MEEREN et al., 2010). It influences occurrence, growth rate, size, and life span of individual species

(HOLMES, 2001). Here, *C. trapeziformis*, *C. vidua* and *P. karamani* are indicator species for low water temperatures. These species were found in waters with a maximum temperature of 14.8°C, and their temperature tolerances were very narrow (0.7-1.5°C) (Fig. 4).

Another factor known to affect ostracod distribution is nutrient status; in spite of the inclusion of hypereutrophic lakes in the dataset, nutrient variables were not identified as significant in forward selection. The low and rather stable nutrient status in oligotrophic Lake Ohrid and in all sampled spring habitats may be responsible for this insensitivity.

The clear distinction between Lake Ohrid and water bodies in its surroundings, as indicated by SIMPER (Table 1S, supplementary material), is not surprising because of the high level of endemism. But this distinction underlines that paleoreconstruction will have to rely mainly on modern ecological distribution within the lake itself. More detailed studies of seasonality and niche requirements of key taxa are required, and a more extensive regional training set would be of little value for improving reconstructions.

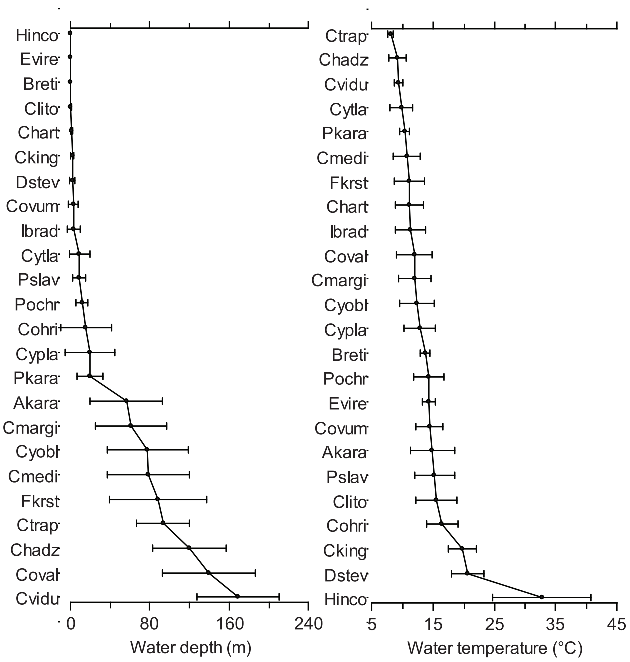

Fig. 4. –Ostracod species optima and tolerance ranges for water depth and water temperature estimated by weighted averaging (WA) regression.

CONCLUSIONS

A comprehensive investigation of ostracod distribution in a variety of aquatic habitat types (lakes, springs, rivers, and channels) in the southeastern Balkan Peninsula retrieved a total of 47 ostracod species (40 living species and seven species detected by valves and empty carapaces) belonging to 18 genera and seven families (Candonidae, Ilyocyprididae, Cyprididae, Leptocytheridae, Limnocytheridae, Cytherideidae, and Darwinulidae). *C. obliqua*, *Cypria lacustris*, *C. media*, and *A. karamani* were the most common species. Short-lived seasonal water bodies, channels, ditches, rivers, and springs were characterized by widespread species such as *H. incongruens*, *Heterocypris reptans* (Baird, 1835), *C. kingsleii*, and *Psychrodromus fontinalis* (Wolf, 1920). The ostracod composition of Lake Ohrid is highly distinct from its surroundings, with *C. obliqua* being the most abundant species. Species-specific distribution of ostracods is influenced by a complex interconnection of physical-chemical water characteristics. From canonical correspondence analyses, water depth, salinity, conductivity, pH, and dissolved oxygen were the main determining factors for ostracod distribution in the entire study area. Ostracods in Lake Ohrid were mainly controlled by water depth, water temperature, and pH. Some species appeared to be strong indicator species for important environmental variables: *C. trapeziformis*, *C. vidua*, and *P. karamani* for cold waters (<14.8°C, tolerance <1.5°C) and *B. reticulata*, *C. hartmanni*, *C. kingsleii*, *C. litoralis*, *E. virens*, and *H. incongruens* for shallow water depth. Because of the now established autecology of the ostracod species from Lake Ohrid it is possible to use fossil ostracod assemblages from sediment cores as paleoenvironmental indicators, although a more intensive monitoring programme, including wave energy quantification, is necessary to further strengthen understanding.

ACKNOWLEDGEMENTS

We thank Trajan Petkovski (Macedonian Museum of Natural History, Skopje, Macedonia) and Burkhard Scharf (Bremen, Germany) for support with ostracod taxonomy, Dietmar Keyser (Zoologisches Institut und Zoologisches Museum, Hamburg, Germany) and Hanna Ciesynski (Institut für Geologie und Mineralogie, Universität zu Köln, Germany) for SEM pictures, and Martin Wessels (Institut für Seenforschung, Langenargen, Germany) for equipment supply. Furthermore, we are grateful to Philipp Hoelzmann (Institut für Geographische Wissenschaften, Freie Universität Berlin, Germany) and Adelina Calean (Institut für Geoökologie, TU Braunschweig, Germany) for water chemistry analyses. Special thanks go to Dagmar Söndgerath (Institut für Geoökologie, TU Braunschweig, Germany) for her help with statistical analyses and we also thank Hubert Kanafa, Meike List, Burkhard Scharf, and Finn Viehberg for their help during the field campaigns. We are also in debt to Goce Kostoski and Sasho Trajanovski, and, in particular, to Zoran Brdarovski from the Hydrobiological Institute in Ohrid for the support and commitment during the field campaigns, and to Kirstin Föller, Torsten Hauffe, and their team (Spezielle Zoologie und Biodiversitätsforschung, Justus-Liebig-Universität Gießen, Germany) for providing sediment samples. We thank Jane Reed and an anonymous reviewer for constructive comments and Jane Reed for checking the English grammar. This project was funded by the Deutsche Forschungsgemeinschaft (Schw 671/11).

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Received: September 27th, 2012

Accepted: June 3rd, 2013

Branch editor: Eggermont Hilde

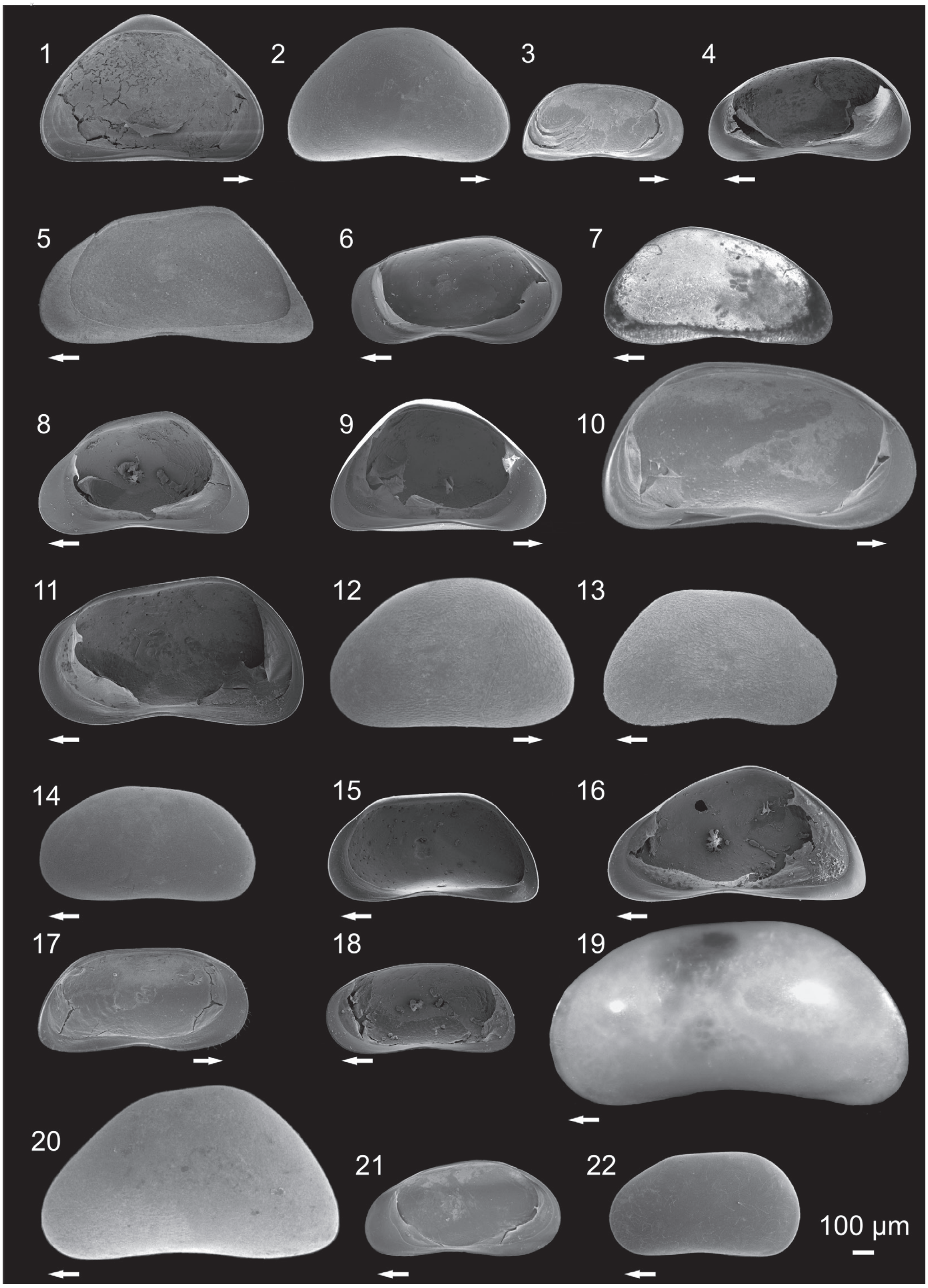

Fig. 1S. – *Candona goricensis* (1) Left valve (LV), internal view, female; *Candona goricensis* (2) Right valve (RV), external view, female; *Candona hadzistei* (3) LV, internal view, male; *Candona hartmanni* (4) RV, internal view, female; *Candona holmesi* (5) RV, internal view, female; *Fabaeformiscandona krstici* (6) RV, internal view, male; *Candona litoralis* (7) LV, external view, male; *Candona margaritana* (8) RV, internal view, female; *Candona margaritana* (9) LV, internal view, female; *Candona marginatoides* (10) LV, internal view, female; *Candona media* (11) RV, internal view, female; *Candona ohrida* (12) RV, external view, male; *Candona ohrida* (13) LV, external view, male; *Candona ovalis* (14) LV, external view, female; *Candona trapeziformis* (15) RV, internal view, female; *Candona triangulata* (16) RV, internal view, female; *Candona vidua* (17) LV, internal view, female; *Candona marginata* (18) RV, internal view, female; *Candona bimucronata* (19) LV, external view, female; *Candona expansa* (20) LV, external view, female; *Candonopsis kingsleii* (21) RV, internal view, male; *Pseudocandona compressa* (22) LV, external view, female. Arrows point to anterior.

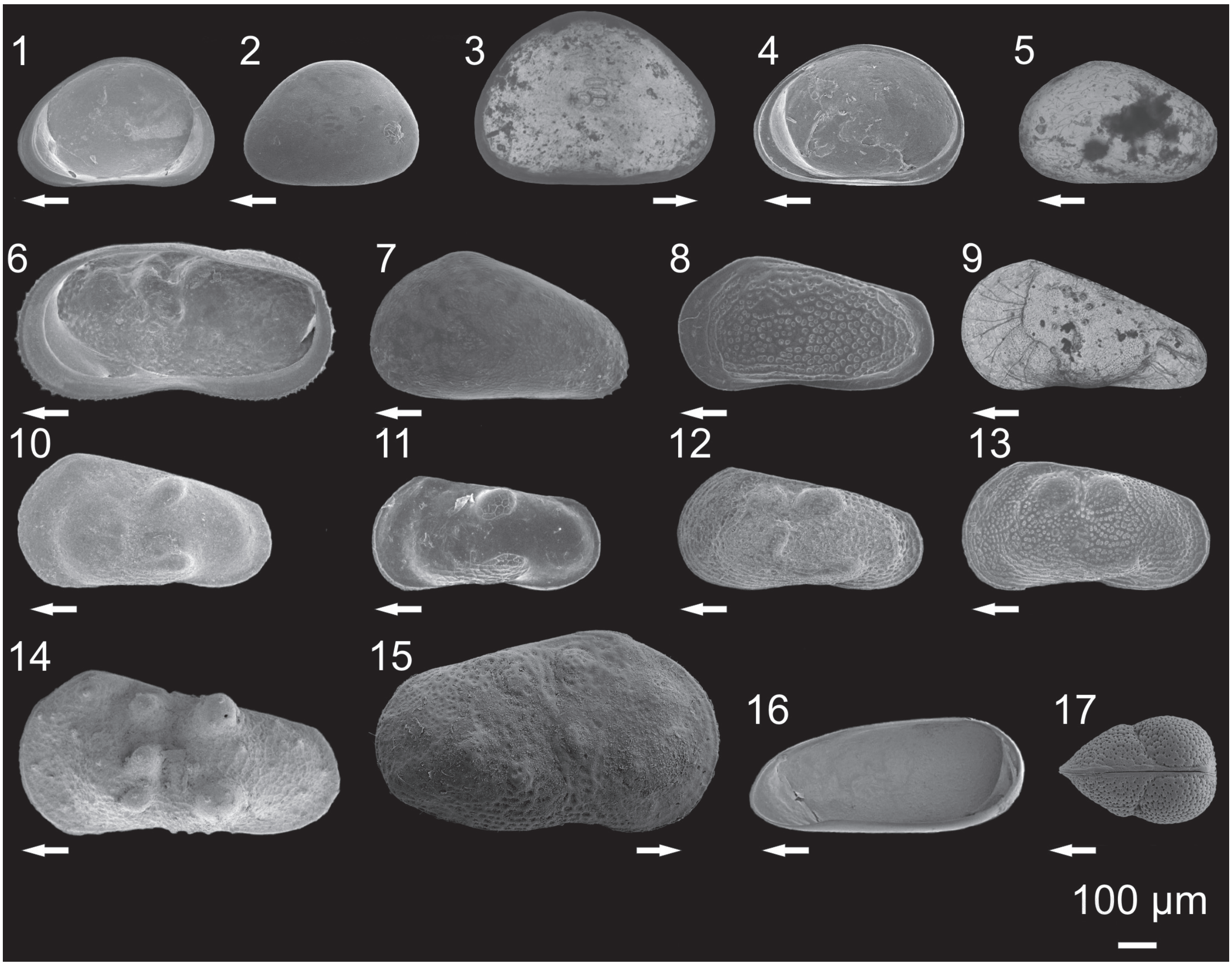

Fig. 2S. – *Cypria lacustris* (1) Right valve (RV), internal view, female; *Cypria obliqua* (2) Left valve (LV), external view, female; *Cypria ophtalmica* (3) LV, internal view, isolated valve; *Cyclocypris ovum* (4) RV, internal view, female; *Heterocypris salina* (5) LV, external view, isolated valve; *Ilyocypris bradyi* (6) RV, internal view, female; *Prionocypris zenkeri* (7) LV, external view, juvenile; *Amnicythere karamani* (8) LV, external view, female; *Paralimnocythere alata* (9) LV, external view, female; *Paralimnocythere georgevitschi* (10) LV, external view, female; *Paralimnocythere karamani* (11) LV, external view, female; *Paralimnocythere ochridense* (12) LV, external view, female; *Paralimnocythere slavei* (13) LV, external view, female; *Paralimnocythere umbonata* (14) LV, external view, female; *Cytherissa lacustris* (15) RV, external view, female; *Darwinula stevensoni* (16) RV, internal view, female; *Kovalevskiella* sp. (17) dorsal view, female. Arrows point to anterior.

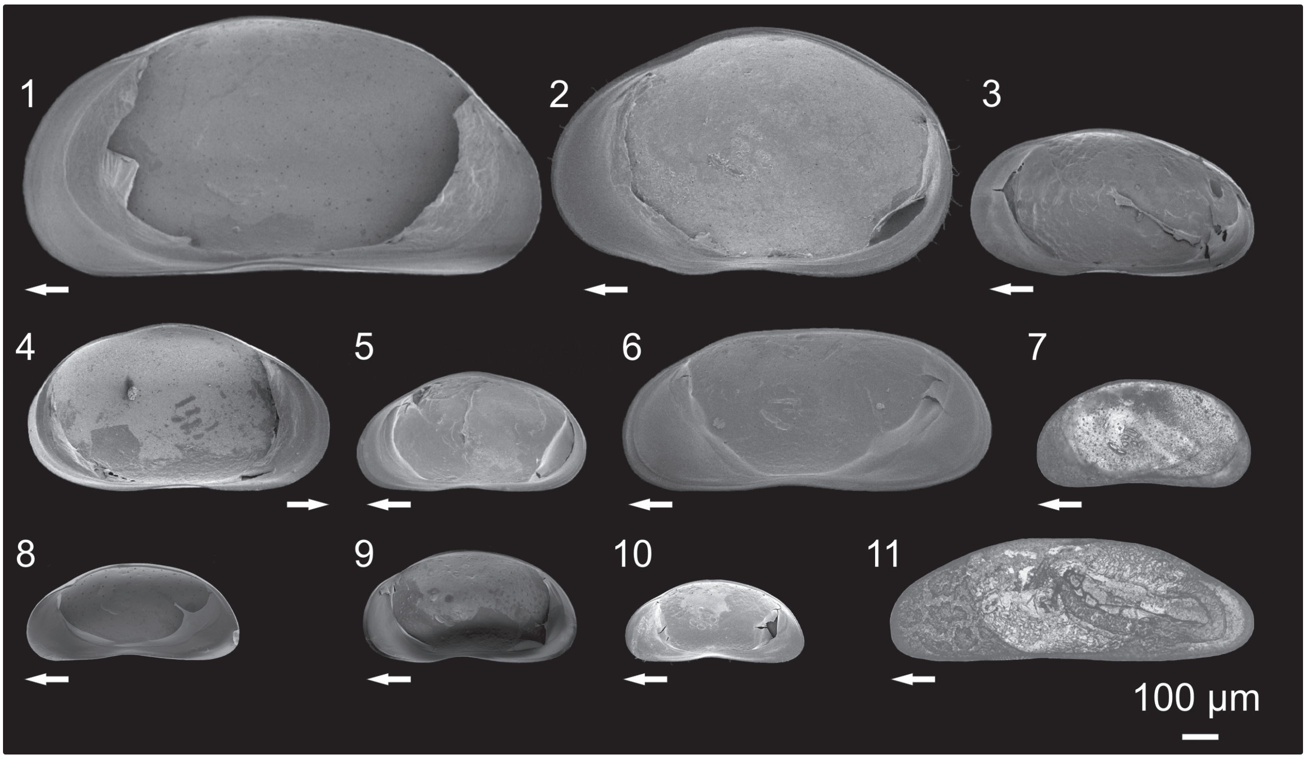

Fig. 3S. – *Eucypris* sp. (1) Right valve (RV), internal view, female; *Eucypris virens* (2) RV, internal view, female; *Bradleystrandesia reticulata* (3) RV, internal view, female; *Heterocypris incongruens* (4) Left valve (LV), internal view, female; *Heterocypris reptans* (5) RV, internal view, female; *Herpetocypris* sp. (6) RV, internal view, female; *Herpetocypris* sp. 2 (7) LV, external view, female; *Psychrodromus fontinalis* (8) RV, internal view, female; *Psychrodromus olivaceus* (9) RV, internal view, female; *Psychrodromus* sp. (10) RV, internal view, female; *Dolerocypris sinensis* (11) LV, external view, female. Arrows point to anterior.

Fig. 4S. – Distribution maps of the 40 living ostracod species in the study area (A) and in Lake Ohrid (B). Species codes as in Table 1.

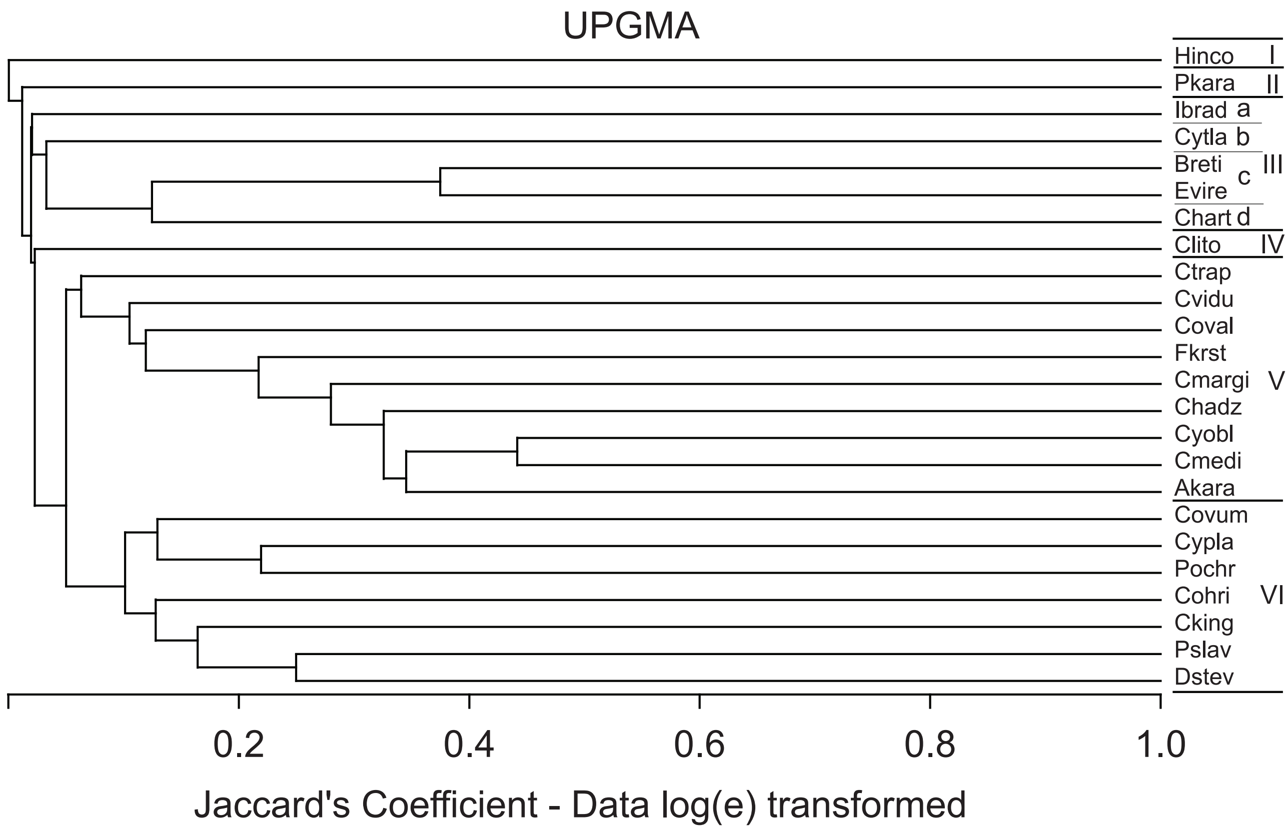

Fig. 5S. – Dendrogram for the unweighted pair group mean average (UPGMA) for the entire dataset. Roman numerals and characters after species codes (as in Table 1) indicate the clustering groups.

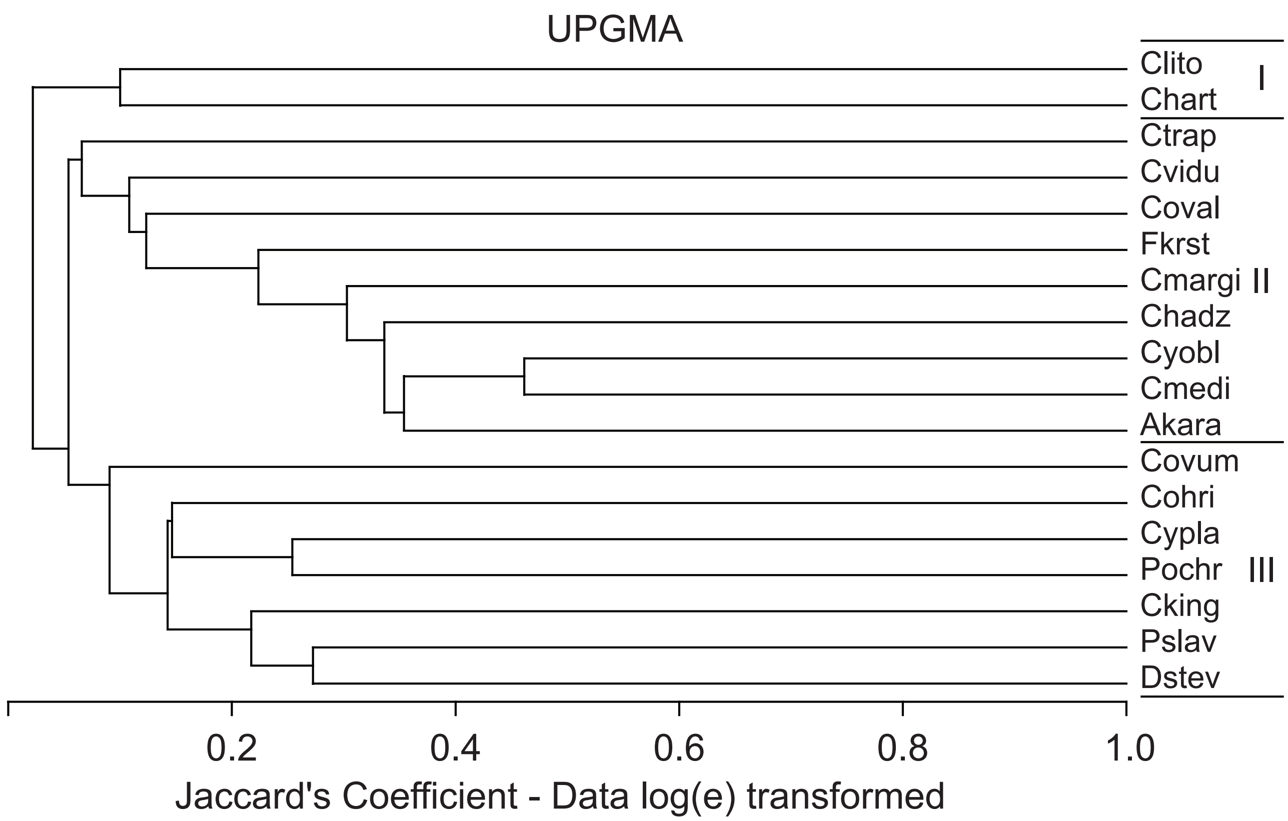

Fig. 6S. – Dendrogram for the unweighted pair group mean average (UPGMA) for the Lake-Ohrid dataset. Roman numerals after species codes (as in Table 1) indicate the clustering groups.

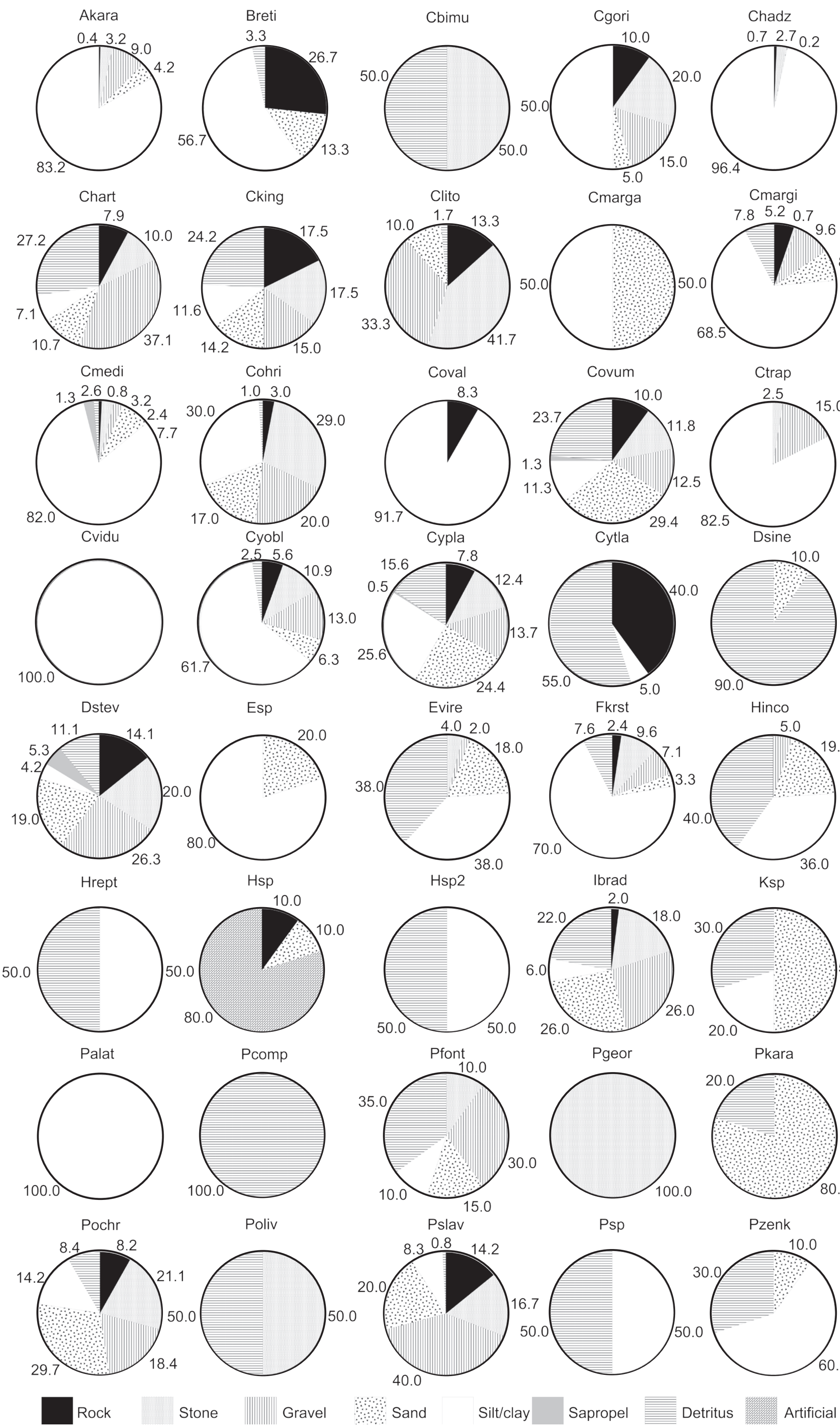

Fig. 7S. – Pie diagram showing the average sediment composition at the sampling locations for the 40 living ostracod species. Species codes as in Table 1.

TABLE 1S

Summary of the similarity percentage (SIMPER) analysis for the first five main ostracod species contributing to the average dissimilarity between habitats (Diss. contr.: Dissimilarity contribution, Cum. diss.: Cumulative dissimilarity, and Av. diss.: Average dissimilarity).

Ohrid vs. channel	**Diss. contr. (%)**	**Cum. diss. (%)**	**Ohrid vs. ditches**	**Diss. contr. (%)**	**Cum. diss. (%)**	**Ohrid vs. lakes**	**Diss. contr. (%)**	**Cum. diss. (%)**
Cypla	43.85	49.56	Cyobl	21.54	23.06	Cypla	28.76	32.48
Cyobl	21.54	73.91	Cypla	21.18	45.73	Cyobl	21.54	56.80
Akara	3.38	77.73	Cking	13.88	60.59	Dstev	9.78	67.85
Cmargi	2.69	80.78	Breti	10.13	71.44	Akara	6.30	74.97
Pochr	2.68	83.80	Cmargi	6.61	78.52	Cmedi	4.78	80.36
Av. diss.: 88.48%			**Av. diss.: 93.40%**			**Av. diss.: 88.55%**		
Ohrid vs. flooded areas	**Diss. contr. (%)**	**Cum. diss. (%)**	**Ohrid vs. rivers**	**Diss. contr. (%)**	**Cum. diss. (%)**	**Ohrid vs. springs**	**Diss. contr. (%)**	**Cum. diss. (%)**
Hinco	25.00	25.47	Cyobl	21.54	22.72	Cyobl	21.54	23.23
Cyobl	21.54	47.42	Cypla	16.76	40.40	Cypla	20.26	45.08
Ibrad	9.75	57.35	Cking	14.30	55.48	Covum	10.59	56.51
Pochr	6.70	64.18	Cmedi	8.88	64.84	Pochr	5.69	62.65
Evire	6.33	70.63	Covum	7.91	73.18	Pslav	5.44	68.51
Av. diss.: 98.15%			**Av. diss.: 94.81%**			**Av. diss.: 92.73%**		
Channels vs. ditches	**Diss. contr. (%)**	**Cum. diss. (%)**	**Channels vs. lakes**	**Diss. contr. (%)**	**Cum. diss. (%)**	**Channels vs. flooded areas**	**Diss. contr. (%)**	**Cum. diss. (%)**
Cypla	29.48	49.49	Cypla	18.71	49.17	Cypla	49.60	49.80
Cking	13.58	72.28	Dstev	9.04	72.91	Hinco	25.00	74.90
Breti	10.06	89.17	Akara	4.00	83.42	Ibrad	9.71	84.65
Cmargi	4.78	97.19	Cmedi	3.33	92.18	Evire	6.19	90.86
Cytla	0.78	98.50	Covum	1.32	85.64	Pochr	4.67	95.55
Av. diss.: 59.57%			**Av. diss.: 38.05%**			**Av. diss.: 99.60%**		
Channels vs. rivers	**Diss. contr. (%)**	**Cum. diss. (%)**	**Channels vs. springs**	**Diss. contr. (%)**	**Cum. diss. (%)**	**Ditches vs. lakes**	**Diss. contr. (%)**	**Cum. diss. (%)**
Cypla	35.54	49.60	Cypla	29.88	49.46	Cypla	25.54	34.55
Cking	13.90	69.00	Covum	10.08	66.15	Cking	13.58	52.91
Cmedi	7.53	79.51	Pslav	4.29	73.25	Breti	10.06	66.53

Clito	7.14	89.48	Pochr	3.61	79.22	Dstev	9.04	78.75
Covum	7.14	99.45	Chart	2.78	83.82	Cmargi	4.94	85.43
Av. diss.: 71.66%			**Av. diss.: 60.40%**			**Av. diss.: 73.92%**		
Ditches vs. flooded areas	**Diss. contr. (%)**	**Cum. diss. (%)**	**Ditches vs. rivers**	**Diss. contr. (%)**	**Cum. diss. (%)**	**Ditches vs. springs**	**Diss. contr. (%)**	**Cum. diss. (%)**
Hinco	25.00	25.35	Cypla	22.99	28.56	Cypla	23.35	28.62
Cypla	20.31	45.94	Cking	19.72	53.06	Cking	13.94	45.71
Cking	13.58	59.70	Breti	10.06	65.56	Covum	10.11	58.10
Breti	10.11	69.95	Cmedi	7.58	74.97	Breti	10.08	70.45
Ibrad	9.77	79.86	Covum	7.34	84.08	Cmargi	4.79	76.32
Av. diss.: 98.63%			**Av. diss.: 80.50%**			**Av. diss.: 81.58%**		
Lakes vs. flooded areas	**Diss. contr. (%)**	**Cum. diss. (%)**	**Lakes vs. rivers**	**Diss. contr. (%)**	**Cum. diss. (%)**	**Lakes vs. springs**	**Diss. contr. (%)**	**Cum. diss. (%)**
Cypla	31.05	31.34	Cypla	27.59	34.16	Cypla	23.23	33.27
Hinco	25.00	56.58	Cking	13.90	51.37	Dstev	10.60	48.46
Ibrad	9.71	66.38	Cmedi	9.76	63.45	Covum	10.35	63.28
Dstev	9.04	75.50	Dstev	9.04	74.63	Pslav	4.29	69.41
Evire	6.19	81.75	Covum	8.08	84.64	Pochr	4.23	75.48
Av. diss.: 99.07%			**Av. diss.: 80.77%**			**Av. diss.: 69.82%**		
Flooded areas vs. rivers	**Diss. contr. (%)**	**Cum. diss. (%)**	**Flooded areas vs. springs**	**Diss. contr. (%)**	**Cum. diss. (%)**	**Rivers vs. springs**	**Diss. contr. (%)**	**Cum. diss. (%)**
Hinco	25.00	25.01	Hinco	25.00	25.29	Cypla	22.80	26.87
Cypla	14.29	39.30	Cypla	19.87	45.40	Cking	14.57	44.04
Cking	13.90	53.21	Covum	10.08	55.60	Covum	14.34	60.95
Ibrad	9.71	62.93	Ibrad	9.72	65.43	Cmedi	7.53	69.82
Cmedi	7.56	70.49	Pochr	7.43	72.94	Clito	7.14	78.24
Av. diss.: 99.96%			**Av. diss.: 98.84%**			**Av. diss.: 84.86%**		

TABLE 2S

Pearson correlation between pairs of environmental variables and habitat types for the entire dataset. Variables with high correlations (+/-0.7-1.0) are bold and underlined and correlations between 0.6-0.7 are bold.

	Salinity	Depth	DO	Temp	pH	SO_4	PO_4	NH_4	NO_2	NO_3	Cond	Ca	Fe	Mg	K	Na	Mn	Sr	Cl	DOC	Ohrid	Channel	Ditch	Lake	Flooded	River	Spring	Rocks	Stones	Gravel	Sand	Silt	Sapropel	Detritus
Salinity	1.00																																	
Depth	-0.18	1.00																																
DO	-0.10	0.08	1.00																															
Temp	0.03	-0.23	0.35	1.00																														
pH	0.09	0.17	0.51	0.54	1.00																													
SO_4	-0.16	0.32	0.37	0.06	0.32	1.00																												
PO_4	0.18	0.00	0.07	-0.02	0.00	-0.02	1.00																											
NH_4	-0.11	0.18	0.05	-0.06	-0.01	0.23	0.06	1.00																										
NO_2	-0.04	-0.02	-0.09	-0.09	-0.13	0.00	0.10	**0.84**	1.00																									
NO_3	-0.07	0.16	0.08	-0.07	0.07	0.17	0.00	0.05	0.03	1.00																								
Cond	0.27	0.03	0.33	0.34	0.29	0.11	0.05	0.02	-0.05	0.07	1.00																							
Ca	-0.05	0.12	0.26	-0.06	0.22	0.41	-0.05	0.04	-0.03	-0.09	0.04	1.00																						
Fe	-0.09	0.04	0.24	-0.08	0.18	0.26	-0.04	-0.08	-0.04	-0.07	0.00	**0.73**	1.00																					
Mg	-0.10	0.12	0.28	-0.05	0.22	0.42	-0.05	0.05	-0.03	-0.09	0.03	**0.98**	**0.71**	1.00																				
K	-0.10	0.10	0.28	-0.03	0.22	0.42	-0.05	0.07	-0.03	-0.09	0.03	**0.96**	**0.68**	**0.98**	1.00																			
Na	-0.09	0.12	0.27	-0.04	0.21	0.42	-0.05	0.07	-0.03	-0.09	0.03	**0.95**	**0.66**	**0.98**	**0.99**	1.00																		
Mn	-0.07	0.09	0.18	-0.09	0.16	0.20	-0.03	-0.07	-0.03	-0.06	0.01	**0.65**	**0.92**	**0.60**	0.56	0.51	1.00																	
Sr	-0.09	0.12	0.27	-0.05	0.22	0.42	-0.05	0.05	-0.03	-0.09	0.03	**0.98**	**0.72**	**1.00**	**0.98**	**0.98**	**0.61**	1.00																
Cl	-0.10	0.37	0.31	-0.06	0.19	0.45	0.09	0.15	-0.02	0.00	0.08	0.24	0.17	0.24	0.24	0.25	0.13	0.24	1.00															
DOC	-0.07	0.11	0.20	-0.02	0.18	0.30	-0.04	0.07	-0.02	-0.07	0.04	**0.74**	0.25	**0.77**	**0.73**	**0.72**	0.23	**0.76**	0.18	1.00														
Ohrid	-0.46	0.37	0.30	0.14	0.32	0.32	-0.09	0.01	-0.11	0.01	-0.21	0.21	0.18	0.24	0.24	0.23	0.15	0.23	0.21	0.18	1.00													
Channel	-0.05	-0.11	-0.06	-0.10	-0.09	-0.08	0.03	0.33	0.40	0.04	-0.04	-0.08	-0.05	-0.08	-0.07	-0.07	-0.05	-0.08	-0.09	-0.06	-0.30	1.00												
Ditch	-0.04	-0.10	-0.12	-0.06	-0.28	-0.12	-0.02	-0.06	-0.02	-0.04	0.12	-0.07	-0.05	-0.07	-0.07	-0.07	-0.04	-0.07	-0.08	-0.05	-0.27	-0.03	1.00											
Lake	-0.04	-0.10	-0.12	0.05	0.00	0.04	-0.01	0.03	-0.01	-0.04	-0.01	-0.07	-0.05	-0.07	-0.07	-0.07	-0.04	-0.07	-0.03	-0.05	-0.27	-0.03	-0.02	1.00										
Flooded	0.22	-0.13	-0.08	-0.04	-0.26	-0.15	-0.02	-0.08	-0.03	-0.05	0.07	-0.09	-0.06	-0.09	-0.09	-0.09	-0.05	-0.09	-0.10	-0.07	-0.35	-0.03	-0.03	-0.03	1.00									
River	-0.05	-0.12	-0.20	-0.04	-0.07	-0.14	-0.01	0.01	0.02	0.05	0.12	-0.08	-0.06	-0.08	-0.08	-0.08	-0.05	-0.08	-0.09	-0.06	-0.32	-0.03	-0.03	-0.03	-0.04	1.00								
Springs	**0.62**	-0.21	-0.11	-0.09	-0.06	-0.20	0.15	-0.13	-0.05	0.00	0.14	-0.08	-0.10	-0.12	-0.13	-0.11	-0.09	-0.12	-0.08	-0.09	-0.58	-0.06	-0.05	-0.05	-0.07	-0.06	1.00							
Rocks	0.18	-0.18	-0.07	0.19	0.00	-0.12	-0.03	-0.09	-0.02	-0.05	0.02	-0.12	-0.09	-0.13	-0.12	-0.12	-0.07	-0.13	-0.14	-0.10	-0.13	-0.05	0.12	0.04	-0.06	0.03	0.15	1.00						
Stones	0.08	-0.25	-0.04	0.13	-0.04	0.03	-0.05	-0.12	-0.02	-0.07	-0.03	-0.18	-0.13	-0.18	-0.17	-0.17	-0.11	-0.18	-0.16	-0.14	0.03	-0.07	-0.06	0.06	-0.08	0.03	0.03	0.15	1.00					
Gravel	0.00	-0.26	-0.09	0.10	-0.15	-0.19	-0.05	-0.15	-0.04	-0.09	-0.03	-0.20	-0.14	-0.20	-0.20	-0.20	-0.12	-0.20	-0.23	-0.16	0.00	-0.01	-0.03	-0.04	0.03	0.03	0.00	0.00	0.28	1.00				
Sand	0.22	-0.29	-0.12	-0.03	-0.14	-0.16	-0.05	-0.11	-0.01	0.02	0.08	-0.13	-0.15	-0.18	-0.18	-0.17	-0.12	-0.17	-0.15	-0.13	-0.43	0.01	0.04	0.12	0.16	0.20	0.32	-0.05	0.02	0.19	1.00			
Silt	-0.15	**0.77**	0.02	-0.28	-0.04	0.20	0.05	0.19	0.07	0.24	0.09	-0.06	-0.10	-0.07	-0.08	-0.07	0.00	-0.06	0.26	-0.02	0.13	0.07	0.01	-0.09	0.04	-0.09	-0.16	-0.18	-0.25	-0.26	-0.18	1.00		
Sapropel	-0.02	-0.05	-0.08	0.11	0.04	0.04	0.00	0.05	0.01	-0.02	0.06	-0.04	-0.03	-0.04	-0.04	-0.04	-0.02	-0.04	0.07	-0.03	-0.14	-0.01	-0.01	0.43	-0.02	-0.02	0.02	-0.02	-0.03	-0.02	-0.02	-0.05	1.00	
Detritus	0.26	-0.23	-0.18	-0.10	-0.11	-0.24	-0.03	-0.02	0.06	-0.06	0.01	-0.14	-0.11	-0.15	-0.15	-0.15	-0.09	-0.15	-0.17	-0.11	-0.40	0.14	0.06	-0.01	0.24	-0.02	0.33	0.02	-0.07	-0.08	0.10	-0.11	-0.02	1.00

TABLE 3S

Pearson correlation between pairs of environmental variables for the Lake-Ohrid dataset. Variables with high correlations (+/-0.7-1.0) are bold and underlined and correlations between 0.6-0.7 are bold.

	Depth	Salinity	DO	Temp	pH	SO_4	PO_4	NH_4	NO_2	NO_3	Cond	Ca	Fe	Mg	K	Na	Mn	Sr	Cl	DOC	Rocks	Stones	Gravel	Sand	Silt	Detritus
Depth	1.00																									
Salinity	-0.06	1.00																								
DO	-0.04	-0.13	1.00																							
Temp	-0.36	0.09	0.29	1.00																						
pH	0.08	0.04	0.53	0.53	1.00																					
SO_4	0.24	-0.07	0.31	-0.04	0.27	1.00																				
PO_4	0.05	-0.01	0.14	-0.02	0.02	-0.06	1.00																			
NH_4	0.35	-0.05	0.22	-0.04	0.14	0.44	-0.04	1.00																		
NO_2	0.19	-0.04	0.09	0.12	0.15	0.44	0.01	0.47	1.00																	
NO_3	0.18	-0.02	0.09	-0.12	0.04	0.21	0.02	0.00	0.01	1.00																
Cond	0.21	-0.03	0.58	0.24	0.54	0.37	0.05	0.29	0.25	0.11	1.00															
Ca	0.05	0.04	0.24	-0.12	0.21	0.38	-0.05	0.10	-0.04	-0.10	0.15	1.00														
Fe	-0.02	-0.03	0.23	-0.12	0.17	0.23	-0.04	-0.14	-0.13	-0.08	0.07	**0.75**	1.00													
Mg	0.04	-0.04	0.25	-0.10	0.21	0.38	-0.05	0.10	-0.04	-0.10	0.15	**0.99**	**0.70**	1.00												
K	0.02	-0.04	0.26	-0.08	0.20	0.39	-0.05	0.13	-0.01	-0.10	0.15	**0.97**	**0.67**	**0.98**	1.00											
Na	0.04	-0.04	0.25	-0.09	0.18	0.39	-0.05	0.14	0.00	-0.10	0.15	**0.95**	**0.65**	**0.98**	**0.99**	1.00										
Mn	0.04	-0.02	0.17	-0.13	0.16	0.17	-0.03	-0.14	-0.13	-0.07	0.07	**0.66**	**0.92**	0.59	0.55	0.50	1.00									
Sr	0.05	-0.04	0.25	-0.11	0.21	0.38	-0.05	0.11	-0.03	-0.10	0.15	**0.99**	**0.71**	**1.00**	**0.98**	**0.98**	**0.60**	1.00								
Cl	0.34	-0.05	0.29	-0.14	0.15	0.43	0.22	0.29	0.09	-0.08	0.23	0.20	0.14	0.21	0.21	0.21	0.11	0.21	1.00							
DOC	0.06	-0.03	0.18	-0.05	0.17	0.26	-0.04	0.14	-0.01	-0.08	0.14	**0.73**	0.23	**0.76**	**0.71**	**0.71**	0.21	**0.75**	0.15	1.00						
Rocks	-0.19	-0.02	0.01	0.26	0.07	-0.07	-0.02	-0.11	0.08	-0.04	0.08	-0.13	-0.09	-0.13	-0.13	-0.13	-0.08	-0.13	-0.14	-0.10	1.00					
Stones	-0.31	-0.03	0.10	0.17	-0.11	-0.04	-0.04	-0.20	0.11	-0.07	-0.01	-0.21	-0.15	-0.21	-0.21	-0.20	-0.12	-0.21	-0.23	-0.16	0.24	1.00				
Gravel	-0.31	-0.04	0.14	0.17	-0.26	-0.22	-0.04	-0.24	-0.05	-0.09	0.00	-0.23	-0.16	-0.23	-0.23	-0.23	-0.14	-0.23	-0.25	-0.18	0.05	0.27	1.00			
Sand	-0.28	-0.03	0.08	0.09	-0.20	-0.11	-0.04	-0.15	0.02	-0.06	0.03	-0.20	-0.14	-0.20	-0.20	-0.20	-0.12	-0.20	-0.22	-0.15	-0.02	0.11	0.34	1.00		
Silt	**0.83**	-0.02	0.05	-0.35	-0.03	0.20	0.15	0.26	0.10	0.28	0.20	-0.08	-0.14	-0.10	-0.12	-0.10	-0.02	-0.10	0.29	-0.04	-0.16	-0.26	-0.28	-0.16	1.00	
Detritus	-0.15	0.36	-0.09	-0.01	0.00	-0.14	-0.02	-0.05	-0.09	-0.03	0.04	-0.10	-0.07	-0.10	-0.10	-0.10	-0.06	-0.10	-0.11	-0.08	-0.02	0.01	-0.05	0.06	-0.10	1.00

TABLE 4S

Estimated optima, tolerance ranges, and standard errors (SE) for significant variables determined with weighted averaging (WA) model. Abbreviations for species see Table 1.

Species	**Water depth (m)**				**Water temperature (°C)**				**Salinity (‰)**				**pH**				**DO (mgl^{-1})**				**Conductivity (μScm^{-1})**			
code	Opt	Tol	SE_ Opt	SE_ Tol	Opt	Tol	SE_ Opt	SE_ Tol	Opt	Tol	SE_ Opt	SE_ Tol	Opt	Tol	SE_ Opt	SE_ Tol	Opt	Tol	SE_ Opt	SE_ Tol	Opt	Tol	SE_ Opt	SE_ Tol
Akara	56.7	73	14.7	12.2	14.9	7.1	1.6	0.5	0.00	0.04	0.00	0.00	8.29	0.46	0.08	0.06	9.3	1.6	0.4	0.4	232.9	12.5	2.2	3.9
Breti	0.5	0.1	0.1	13.1	13.7	1.7	1.3	1.4	0.10	0.04	0.00	0.00	9.16	0.43	0.00	0.00	6.2	0.6	0.4	0.7	957.8	245.9	185.6	99.1
Chadz	119.9	74.2	14	5.6	9.2	2.7	0.4	0.6	0.00	0.04	0.00	0.00	8.09	0.37	0.07	0.06	9.2	1.5	0.3	0.2	237.3	5.8	1.1	0.7
Chart	1.3	2.4	0.8	5.3	11.2	4.4	2.2	1.6	0.03	0.05	0.02	0.01	8.87	0.28	0.14	0.10	5.7	5.2	3.1	1.6	311.3	103.5	56.3	35.2
Cking	1.7	3	0.9	1.1	19.8	4.5	1.6	1	0.01	0.04	0.01	0.01	8.56	0.22	0.07	0.07	7.4	2.2	0.9	1.1	411.7	333.8	136.2	158.8
Clito	0.5	1	0.2	5.1	15.5	6.7	3.8	2.7	0.00	0.04	0.00	0.00	8.82	0.31	0.19	0.13	1.4	5.2	3.1	1.7	233.7	0.6	0.4	21
Cmargi	61.1	72.3	13.2	10.9	12.1	5.3	1.4	0.8	0.00	0.02	0.00	0.01	8.28	0.44	0.11	0.04	8.3	2.2	0.5	0.4	245	34.5	9.8	16.4
Cmedi	78.3	83.2	14	7.5	10.8	4.5	0.9	1	0.00	0.01	0.00	0.01	8.24	0.50	0.07	0.06	8.8	2.7	0.6	0.6	244.2	32.6	5.6	11.1
Cohri	15.8	51.6	16.5	28.3	16.5	5.1	1.6	1.4	0.00	0.04	0.00	0.00	8.54	0.32	0.14	0.07	8.9	1.6	0.6	0.6	230.7	6.7	2.7	2.4
Coval	139.6	94.7	29.2	16	12	5.9	2	2.1	0.00	0.04	0.00	0.00	8.10	0.36	0.13	0.07	8.2	1.4	0.4	0.2	236.7	9.7	3.1	2.9
Covum	3.3	8.5	1.5	3.9	14.4	4.5	1	0.7	0.05	0.05	0.01	0.00	8.20	0.62	0.18	0.11	5.8	2.7	1	0.5	343.3	122.1	32.6	35.8
Ctrap	93.6	53.4	24.3	17.5	8.2	0.7	0.4	0.8	0.00	0.04	0.00	0.00	8.00	0.57	0.24	0.23	9.9	0.5	0.3	0.6	232.3	8.1	6.4	11.5
Cvidu	168.7	83.1	25.2	20.3	9.5	1.1	0.4	0.3	0.00	0.04	0.00	0.00	8.04	0.24	0.06	0.09	7.7	1.7	0.7	0.5	241.3	7.8	2.8	1.9
Cyobl	77.9	81.6	8.9	6.7	12.4	5.7	0.5	0.4	0.00	0.01	0.00	0.01	8.37	0.53	0.05	0.04	8.8	1.9	0.2	0.2	234	18.4	2	7
Cypla	19.5	49.9	7.1	16.2	12.9	5.1	0.7	0.4	0.01	0.04	0.00	0.00	8.25	0.52	0.07	0.06	7.7	3.2	0.5	0.5	269	43.8	6.2	4
Cytla	9	20.1	10.5	6.9	9.9	3.7	2	2.2	0.00	0.04	0.00	0.00	8.52	0.48	0.31	0.15	9.3	1.9	1	0.6	257.4	24.3	14	11.5
Dstev	2.3	3.8	0.9	0.9	20.6	5.3	1.4	1.4	0.00	0.04	0.00	0.00	8.62	0.26	0.06	0.08	7.9	3.1	0.8	0.7	239.1	35.3	10.2	11.6
Evire	0.3	0.2	0.1	8.9	14.4	2	1	0.8	0.10	0.06	0.04	0.02	9.13	0.36	0.25	0.16	6.5	1.3	0.9	0.9	604.2	207.5	132.1	81.3
Fkrst	88.5	97.3	27.9	14.2	11.2	4.9	1.7	1	0.00	0.04	0.00	0.00	8.28	0.53	0.18	0.09	8.1	2.4	0.6	0.5	238.3	10.7	3.1	2.8
Hinco	0.1	0.1	0	13.5	32.8	16.1	10.6	5.2	0.10	0.07	0.04	0.01	8.12	0.14	0.09	0.15	8.5	0.3	0.2	0.9	458	140	83.2	42.8
Ibrad	3.6	12.3	8.2	7.1	11.3	5	2.9	2.2	0.09	0.04	0.03	0.02	7.94	0.18	0.19	0.18	4.8	2.2	1.7	1.1	337.8	52.5	38.2	21.7
Pkara	19.9	26.7	14.8	9.4	10.4	1.5	0.9	0.9	0.05	0.07	0.04	0.01	8.54	1.13	0.58	0.42	7.4	2.7	1.5	1.1	264.5	67.3	34.7	24
Pochr	11.5	12.9	2.8	1.4	14.3	5	0.9	0.6	0.01	0.04	0.01	0.01	8.64	0.74	0.19	0.13	8.2	2.3	0.6	0.4	252.4	39.4	10.5	5.9
Pslav	9.2	11.6	3.5	2.9	15.3	6.6	2.4	1.3	0.00	0.04	0.00	0.00	8.29	0.37	0.14	0.07	8.4	1.8	0.8	0.4	260.3	45	20	13.3