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Feeding spectra of bivalve mollusks *Unio* and *Dreissena* from Kanevskoe Reservoir, Ukraine: are they food competitors or not?

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Abstract

Background: One of the most abundant freshwater invaders is *Dreissena polymorpha* which provide wide-ranging direct and indirect impacts on the invaded ecosystems. A particularly notable impact on benthic communities is the extinction of native mollusks of the order Unionida. However, the settlement of *D. polymorpha* on unionid's shells in Kanevskoe Reservoir did not increase native unionid mortality. Since the reason for the successful coexistence of native unionids and invading dreissenids in Kanevskoe Reservoir is unknown, we hypothesized that these mollusks have different feeding spectra. To evaluate this hypothesis, we compared feeding spectra of the mollusks using a fatty acid (FA) marker analysis.

Results: Significant differences in the number and percentages of FAs were found among the mollusks and their food sources, seston, and sediments. Analyses of FA trophic markers in mollusk tissues showed that *U. tumidus* and *Dreissena* species mainly consumed algae (greens, diatoms, and dinoflagellates), cyanobacteria, and detritus particles enriched with bacteria. According to the multivariate statistical analysis, the mollusks had different feeding spectra: *Dreissena* species fed on planktonic sources, while *U. tumidus* mostly consumed food sources of benthic origin, mainly detritus. In addition, *U. tumidus* and *Dreissena* species differed in percentages of long-chain polyunsaturated FAs of n-3 and n-6 families and specific FAs which they could synthesize (20:1n-13 and 22:3 Δ7,13,16).

Conclusions: *U. tumidus* and *Dreissena* species obviously obtained foods of different qualities. *Dreissena* consumed plankton species, i.e., more-valuable food, while *U. tumidus* fed on detritus and phytobenthic species which were of a lower food quality in terms of levels of physiologically important eicosapentaenoic and docosahexaenoic fatty acids. We concluded that the different feeding spectra of mollusks and adaptations of *U. tumidus*, the synthesis of specific FAs, might be the basis for the successful coexistence of native species and invaders for a long time.

Keywords: Invertebrates; Fatty acids; Ration; Invader

Background

Species introductions are now some of the most important human impacts on the world's ecosystems (Strayer et al. 2004). One of the most abundant freshwater invaders is the zebra mussel *Dreissena polymorpha* (Pallas 1771) which now has a broad geographic range in Europe and North America. Established populations of *D. polymorpha* can have wide-ranging direct and indirect impacts on the invaded ecosystems (Sousa et al. 2011). Commonly observed changes include reductions in phytoplankton (Caraco et al. 1997; Strayer et al. 2008) and zooplankton (Pace et al. 1998; Strayer et al. 2008), increase water clarity (Caraco et al. 1997), changes in fish populations (Karatayev et al. 1997; Strayer et al. 2004), an increase of native bivalve mortality, and restructuring of benthic communities (Molloy et al. 1997; Burlakova et al. 2000; Karatayev et al. 2002).

A particularly notable impact on the benthos is the extinction of native mollusks of the order Unionida (Ricciardi et al. 1995; Jokela and Ricciardi 2008). Unionid mortality is strongly correlated to the *Dreissena* field density

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(Ricciardi et al. 1995). Invasions by dreissenids are thought to cause severe declines in unionids through physical disturbance and/or food competition (Thorp and Casper 2002). However, there are some examples where the negative effects were not so strong. For instance, the fouling of *Unio* by *Dreissena* species in Kievskoe Reservoir, Ukraine, did not cause mass unionid mortality (Kharchenko and Zorina-Sakharova 2002).

Unio tumidus (Philipsson 1788), *D. polymorpha*, and *Dreissena bugensis* (Andrusov 1897) inhabit Kanevskoe Reservoir (Dnieper River basin), Ukraine. *D. bugensis* there prefers soft benthic substrata and very rarely settles on *Unio* specimens, while *D. polymorpha* has actively settled on *U. tumidus* shells for many years. In contrast to most American and European lakes, the settlement of *D. polymorpha* on unionid's shells in Kanevskoe Reservoir did not increase native unionid mortality. Since the reason for the successful coexistence of native unionids and invading dreissenids in Kanevskoe Reservoir is unknown, we hypothesized that these mollusks have different feeding spectra. To evaluate this hypothesis, we compared feeding spectra of *U. tumidus*, *D. polymorpha*, and *D. bugensis* using a fatty acid (FA) marker analysis.

Methods

Study site

Samples were taken in the littoral zone of the upper part of Kanevskoe Reservoir (the Dnieper River, Ukraine) on 9 and 16 June 2010. The studied section of the reservoir is situated in a forest-steppe zone. The sampling site (50°20′N, 30°36′E) was situated in the vicinity of Kiev City (Figure 1). The depth of the sampling site was around 2 m. The bottom of the station was mainly silty sand. The temperature of the surface water on sampling days ranged 22.5°C to 24°C. The main hydrological features of the reservoir are given elsewhere (Starodubtsev and Bogdanets 2012).

Field sampling

Samples were collected as follows. Equal volumes of water from the surface and at 1.3 m in depth were immediately pooled to form a pooled sample of phytoplankton. Then, 0.5 L from the pooled sample was preserved with Lugol's solution and kept in a dark place for 15 days in a cylindrical tube. After 15 days, a siphon draft tube was placed in the middle of the cylinder with sample, and 450 mL was carefully removed. Phytoplankton species from a sample of 50 mL in volume were identified and enumerated in a Nageotte chamber under a microscope (Olympus CX21, Shinjuku, Tokyo, Japan). Zooplankton samples were collected by pouring 50 L of surface water through a 75-μm sieve. Retained materials were placed into individual vials and fixed with 4% formalin. Zooplankton species were identified and enumerated in a Bogorov chamber under a stereomicroscope. Phytobenthic samples were randomly collected from the bottom at the sampling station. During collection, a diver opened a pre-vacuumed and closed plastic tube (with a diameter of 3 cm) very close to the bottom surface. When opening the tube, fine deposited materials were gently aspirated into the tube from the substrata. Phytobenthic species were identified and enumerated in a Nageotte chamber under a microscope. Zoobenthic samples were collected from the bottom using a box-shaped sampler of 0.1 × 0.1 m. Zoobenthic organisms were withdrawn using appropriate forceps in the laboratory and placed into glass vials containing ethanol. Then, zoobenthic species were identified and enumerated under a stereomicroscope.

For the FA analysis, we sampled three bivalve mollusk species, *U. tumidus* ($n = 3$), *D. polymorpha* ($n = 8$), and *D. bugensis* ($n = 2$), and their potential food sources of seston ($n = 6$) and sediments ($n = 3$). Each sample of mollusks consisted of the muscles of eight to ten randomly selected individuals. We collected *Unio* specimens which were fouled by *D. polymorpha*. *D. polymorpha* specimens were taken from various substrata, i.e., *Unio* shells, stones, and sediments, to encompass any possible environmental heterogeneity. *D. bugensis* was collected from sediments. Since it was impossible to thoroughly separate the guts from other parts of the mollusk body, the closing muscles, feet, and part of the mantle of several mollusks were pooled to obtain a sample for the FA analysis. Seston samples were collected from pooled samples of phytoplankton. Sediments were collected like the phytobenthic samples by gently aspirating fine deposited materials from the substrata into plastic tubes. Then, samples of seston and sediments were filtered onto membrane filters with pore size 0.75 to 0.85 μm (Vladipor, Vladimir, Russia) and precovered with a layer of $BaSO_4$ to facilitate the separation of residues. Filters were dried at 35°C for about 30 min. Residues that were separated from the filter and tissue samples were placed into vials containing 2 mL of chloroform/methanol (2: 1, *v*/*v*) and stored at −20°C until further analysis. A visual control showed that 100% of the residue was recovered from the filters.

FA analysis

The methods of lipid extraction, transesterification (methylation) of the lipid extracts, and purification of methyl esters were described by Christie (2003). Briefly, lipids from the samples were extracted with chloroform/methanol (2: 1, *v*/*v*) three times simultaneously with mechanical homogenization of the tissues with glass beads. Before extraction, a definite volume of an internal standard solution (a solution of free 19:0 in chloroform, 0.5 mg/mL, Sigma-Aldrich, St. Louis, MO, USA) was added to the

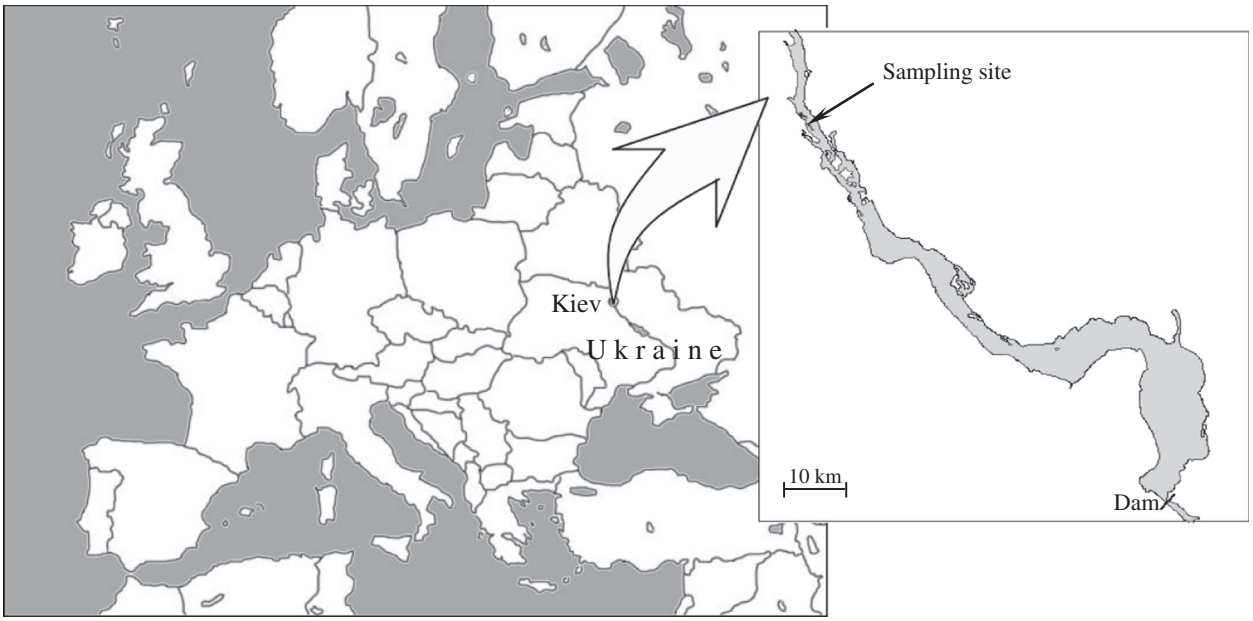

Figure 1 Map of sampling site.

samples. The volume of the internal standard solution that was added to the samples depended on the lipid content of the sample and corresponded to 1 mL/1 g of wet weight of mollusk tissues, 20 μL/1 L of seston, and 100 μL/1 L of sediments. The combined lipid extracts were filtered, dried by passing through an anhydrous Na_2SO_4 layer, and evaporated at 35°C. FA methyl esters (FAMEs) were prepared in a mixture of methanol/sulfuric acid (20: 1, *v*/*v*) at 90°C for 2 h as previously described (Makhutova et al. 2012). FAMEs were analyzed on a gas chromatograph equipped with a mass spectrometer detector (model 6890/5975C, Agilent Technologies, Santa Clara, CA, USA) and a 30-m-long × 0.25-mm internal diameter HP-FFAP capillary column (Agilent Technologies, Santa Clara, CA, USA). The column temperature program was as follows: from 100°C to 190°C at 3°C/min, 5 min isothermally, then to 230°C at 10°C/min, and 20 min isothermally. Other instrument conditions were as described elsewhere (Makhutova et al. 2012). FAME peaks were identified by their mass spectrum compared to those in a database (NIST-2005, Gaithersburg, MD, USA) and to those of available authentic standards (Sigma-Aldrich, St. Louis, MO, USA). Positions of double bonds in monoenoic acids were determined by gas chromatography (GC)-mass spectrometry (MS) of dimethyl disulfide adducts of FAs (Christie 2003). To determine the double bond positions in the polyenoic acids, including non-methylene-interrupted (NMI) FAs, GC-MS of dimethyloxazoline derivatives of FAs was used (Carrido and Medina 2002). FAs that are usually used as biochemical markers of some particular taxonomic groups that occurred in the studied water body are shown in Table 1.

Statistical analysis

The mean, standard error (SE), Fisher's least significant difference (LSD) *post hoc* test, and a canonical correspondence analysis were carried out using STATISTICA software (vers. 9; StatSoft, Tulsa, OK, USA). A canonical correspondence analysis (CCA) was applied to the data matrix that included percentages of prominent FAs of mollusks, seston, and sediments (Table 2). Canonical analyses allow direct comparisons of two data matrices (Legendre and Legendre 2012). Since only 32 prominent acids from 94 identified acids were used in the CCA, the possible influence of 0% and low-percentage entries in the dataset was minimized.

Results

The biomass, abundance, and taxonomic composition of phytoplankton, zooplankton, phytobenthos, and zoobenthos on the sampling days are given in Tables 3 and 4. The content and composition of quantitatively prominent FAs of mollusks, seston, and sediments and FAs of high marker significance are shown in Table 2. In total, 94 FA compounds were identified in all samples.

Using the canonical correspondence analysis, mollusks, seston, and sediments were represented in a two-dimensional space according to the percentages (% of total FAs) of prominent FAs (Figure 2). The first dimension explained 63.5% of the inertia (of the total Chi-square value) of the dataset, and the second dimension explained

Table 1 Fatty acids as biochemical markers of certain taxonomic groups that occur in the studied water body (Kanevskoe Reservoir, Ukraine)

Group	Fatty acid markers	References
Phytoplankton group		
Chlorophyceae	18:2n-6, 18:3n-3, and C16 PUFAs n-3 and n-6	Napolitano 1999
		Viso and Marty 1993
		Petkov and Garcia 2007
Cryptophyceae	Simultaneous occurrence of 18:3n-3 and 18:4n-3; and 20:5n-3 and 22:6n-3	Brett et al. 2009
		Dijkman and Kromkamp 2006
		Desvilettes et al. 1997
		Guevara et al. 2011
Dinophyceae	18:4n-3, 18:5n-3, and 22:6n-3	Napolitano 1999
		Berge and Barnathan 2005
Bacillariophyceae	C16 PUFAs n-7, n-4, n-1, 20:5n-3, and 16:1n-7/16:0 > 1	Dijkman and Kromkamp 2006
		Shin et al. 2000
		Prato et al. 2012
Cyanobacteria	18:3n-3 (or 18:3n-6)	Gugger et al. 2002
Heterotrophic bacteria	Branched C15-17 SFAs and MUFAs, 18:1n-7, 16:1n-6, *trans*-16:1n-5, and 18:1n-8	Napolitano 1999
		Green and Scow 2000
Decomposed material	SFAs, especially 18:0	Hama 1999
Vascular plant detritus	Long-chain SFAs (C20 to C32)	Shorland 1963
		Napolitano 1999
Copepoda	C20 to C22 MUFAs	Hagen et al. 1993
		Kattner et al. 2007
Mollusca	NMI FAs, 20:1n-13, and 22:2n-6	Mezek et al. 2011
		Zhukova 2007
		Saito and Hashimoto 2010

SFAs, saturated fatty acids; MUFAs, monounsaturated fatty acids; PUFAs, polyunsaturated fatty acids; NMI FAs, non-methylene-interrupted fatty acids.

16.6%. Chi-square values for both dimensions and the total Chi-square value were significant ($p = 0.00002$). The first dimension (Figure 2) demonstrated large differences between seston and sediments on one hand, and mollusks on the other. The positioning of samples in the first dimension was mostly provided by differences in their percentages of markers of phytoplankton (C16 polyunsaturated FAs; PUFAs) and markers of vascular plant detritus (C24 to C26 saturated fatty acids; SFAs) that were abundant in seston and sediments on the one hand, and long-chain n-3 and n-6 PUFAs that were abundant in animals, on the other hand (Figure 2, Table 2). The second dimension, although comparatively less substantial, was also significant and indicated differences between *Unio* and *Dreissena* (Figure 2). Differences between mollusks were primarily provided by percentages of 22:4n-6, 20:4n-6, and NMI 22:3 Δ7,13,16 that were high in *Unio* and percentages of 18:1n-7 and 22:6n-3 that were high in *Dreissena* species (Figure 2, Table 2). Seston and sediments also tended to differ in the second dimension (Figure 2). This difference was provided by the percentage of a marker of decomposed material (18:0) that was abundant in sediments and by percentages of markers of phytoplankton (18:2n-6 and 18:3n-3) and bacteria (i15:0) that were abundant in seston (Figure 2, Table 2).

Differences between the percentages of FAs in mollusks and their food items were specified by Fisher's LSD *post hoc* test. Mollusks had significantly higher percentages of taxon-specific markers (20:1n-13, 22:2n-6, and NMI FAs), animal FAs, and long-chain n-3 and n-6 PUFAs compared to seston and sediments (Table 2). In turn, percentages of FA markers of phytoplankton (16:1n-7, 16:1n-9, and C16 PUFAs), zooplankton (22:1n-9), and vascular plant detritus (C24 to C26 SFAs) in seston and sediments were significantly higher than those in mollusks (Table 2). The compositions of bacterial FAs in mollusks were nearly the same as those in seston and sediments (Table 2).

Concerning the FA composition of food sources, seston had significantly higher percentages of markers of phytoplankton (C16 and C18 PUFAs), some bacterial markers (i15:0 and 18:1n-7), and physiologically important PUFAs,

Table 2 Average values of prominent fatty acids and content of FAs in total lipids of mollusks

FAs	Seston			Sediments			*U. tumidus*			*D. polymorpha*			*D. bugensis*		
14:0	5.4	±	0.3^{a}	5.4	±	1.2^{a}	1.0	±	0.0^{b}	1.7	±	0.3^{b}	2.1	±	0.3^{b}
15:0	1.1	±	0.1^{ab}	1.4	±	0.4^{a}	1.2	±	0.0^{ac}	0.8	±	0.1^{bc}	0.7	±	0.1^{bc}
16:0	23.8	±	2.1^{a}	30.3	±	1.0^{b}	16.6	±	0.2^{c}	23.9	±	1.2^{a}	23.1	±	2.0^{ac}
17:0	0.7	±	0.1^{a}	0.8	±	0.2^{a}	2.9	±	0.0^{b}	1.4	±	0.1^{c}	1.0	±	0.1^{ac}
18:0	15.0	±	3.2^{a}	23.5	±	4.7^{b}	9.1	±	0.3^{ac}	5.6	±	0.2^{c}	4.5	±	0.3^{c}
20:0	1.0	±	0.1^{a}	1.2	±	0.1^{a}	0.2	±	0.1^{b}	0.4	±	0.1^{b}	0.7	±	0.0^{ab}
22:0	1.3	±	0.2^{a}	1.7	±	0.5^{a}	0.3	±	0.1^{b}	0.3	±	0.1^{b}	0.2	±	0.0^{b}
24:0	1.3	±	0.2^{a}	1.7	±	0.1^{a}	0.1	±	0.1^{b}	0.2	±	0.1^{b}	0.1	±	0.0^{b}
26:0	0.6	±	0.1^{a}	0.6	±	0.1^{a}	0.0	±	0.0^{b}	0.0	±	0.0^{b}	0.0	±	0.0^{b}
i15:0	1.2	±	0.2^{a}	0.7	±	0.2^{b}	0.1	±	0.0^{c}	0.2	±	0.0^{c}	0.2	±	0.0^{bc}
i17:0	0.6	±	0.1^{ac}	0.4	±	0.1^{a}	1.1	±	0.1^{b}	0.7	±	0.1^{c}	0.7	±	0.1^{ac}
16:1(n-7 + n-9)	10.1	±	0.9^{a}	6.9	±	1.6^{b}	3.4	±	0.2^{c}	4.6	±	0.5^{bc}	6.4	±	0.0^{bc}
18:1n-9	5.2	±	0.7^{ab}	5.4	±	0.6^{ab}	5.9	±	0.3^{a}	4.0	±	0.3^{b}	4.4	±	0.1^{ab}
18:1n-7	2.6	±	0.5^{a}	1.0	±	0.2^{b}	1.0	±	0.1^{b}	2.9	±	0.1^{a}	3.8	±	0.2^{a}
20:1n-13	0.0	±	0.0^{a}	0.0	±	0.0^{a}	13.6	±	0.5^{b}	7.8	±	0.6^{c}	6.4	±	0.3^{c}
20:1n-9	0.5	±	0.1^{a}	0.4	±	0.0^{a}	1.3	±	0.0^{b}	2.7	±	0.2^{c}	1.9	±	0.0^{d}
22:1n-9	2.3	±	0.6^{a}	3.1	±	0.1^{a}	0.3	±	0.0^{b}	0.3	±	0.1^{b}	0.2	±	0.1^{b}
22:1n-7	0.1	±	0.0^{a}	0.0	±	0.0^{a}	0.4	±	0.0^{b}	0.5	±	0.1^{b}	0.4	±	0.1^{b}
16:2n-4	1.4	±	0.2^{a}	0.8	±	0.2^{b}	0.0	±	0.0^{c}	0.1	±	0.0^{c}	0.1	±	0.0^{c}
16:3n-4	1.6	±	0.2^{a}	1.0	±	0.2^{b}	0.0	±	0.0^{c}	0.0	±	0.0^{c}	0.0	±	0.0^{c}
16:4n-3	1.1	±	0.2^{a}	1.0	±	0.3^{a}	0.0	±	0.0^{b}	0.0	±	0.0^{b}	0.1	±	0.0^{b}
18:2n-6	2.1	±	0.2^{a}	1.4	±	0.1^{b}	3.4	±	0.1^{c}	1.5	±	0.1^{b}	2.0	±	0.1^{ab}
18:3n-3	3.3	±	0.5^{a}	1.7	±	0.3^{b}	1.1	±	0.0^{b}	1.9	±	0.1^{b}	5.3	±	0.1^{c}
18:4n-3	2.2	±	0.3^{a}	2.0	±	0.4^{a}	0.3	±	0.0^{b}	0.9	±	0.1^{b}	3.0	±	0.1^{c}
20:4n-6	0.7	±	0.2^{a}	0.3	±	0.0^{a}	8.7	±	0.4^{b}	3.6	±	0.3^{c}	2.2	±	0.4^{d}
20:5n-3	5.1	±	0.7^{a}	2.4	±	0.2^{b}	4.3	±	0.3^{ab}	6.4	±	0.3^{c}	7.7	±	0.7^{c}
22:2n-6	0.0	±	0.0^{a}	0.0	±	0.0^{a}	3.3	±	0.4^{b}	2.9	±	0.2^{b}	2.7	±	0.1^{b}
22:3 Δ7,13,16	0.0	±	0.0^{a}	0.0	±	0.0^{a}	2.0	±	0.3^{b}	0.8	±	0.1^{c}	0.8	±	0.2^{c}
22:4n-6	0.0	±	0.0^{a}	0.0	±	0.0^{a}	2.9	±	0.1^{b}	0.5	±	0.0^{c}	0.3	±	0.0^{d}
22:5n-6	0.7	±	0.1^{a}	0.0	±	0.0^{b}	1.6	±	0.2^{c}	3.3	±	0.2^{d}	1.8	±	0.1^{c}
22:5n-3	0.2	±	0.0^{a}	0.0	±	0.0^{a}	4.9	±	0.1^{b}	5.1	±	0.2^{b}	3.9	±	0.2^{c}
22:6n-3	1.5	±	0.3^{a}	0.0	±	0.0^{b}	1.6	±	0.1^{a}	8.0	±	0.4^{c}	5.1	±	0.4^{d}
BFAs	7.8	±	1.2^{a}	5.4	±	1.5^{a}	6.5	±	0.1^{a}	6.3	±	0.2^{a}	6.7	±	0.3^{a}
FAs, total	nd			nd			3.5	±	0.4^{ab}	3.0	±	0.1^{a}	4.0	±	0.3^{b}

Average values of quantitatively prominent fatty acids (FAs; % of the total, ± SE) of seston ($n = 6$), sediments ($n = 3$), *Unio tumidus* ($n = 3$), *Dreissena polymorpha* ($n = 8$), and *D. bugensis* ($n = 2$), and the content of FAs in total lipids (mg/g wet weight, ± SE) of mollusks from Kanevskoe Reservoir, Ukraine. Means in a row labeled with the same superscript letter do not significantly differ at $p < 0.05$ according to Fisher's LSD **post hoc** test. BFAs, FA markers of bacteria (the sum of i, ai14:0; i, ai15:0; ai15:1; 15:0; i16:0; i17:0; 17:0; and 18:1n-7); nd, not determined.

namely eicosapentaenoic acid (20:5n-3, EPA) and docosahexaenoic acid (22:6n-3, DHA), than sediments (Table 2).

Different species of mollusks differed from each other in percentages of some FAs. *Dreissena* species had higher percentages of FA markers associated with seston, while *Unio* had a higher percentage of stearic acid (18:0), which was abundant in sediments (Table 2). In addition, *Unio* had significantly higher percentages of markers of mollusks (Table 1) and n-6 PUFAs and lower percentages of n-3 PUFAs and the bacterial 18:1n-7, than *Dreissena* species (Table 2). *D. polymorpha* differed from *D. bugensis* mostly by higher percentages of C20-22 PUFAs and lower percentages of C18 PUFAs (Table 2).

Table 3 Abundance, biomass, and taxonomic composition of phytoplankton and phytobenthos from Kanevskoe Reservoir, Ukraine

	Date	Number	Total abundance (10^3 cells/L)	Total biomass (mg/L)	Order	Percent total abundance	Percent total biomass	Dominant species
Phytoplankton	9 June 2010	7	780	0.407	Dinophyta	2.3	72.3	*Gymnodinium* sp.
					Bacillariophyta	16.7	24.5	
					Chlorophyta	81.0	3.2	
	16 June 2010	12	10,560	6.68	Bacillariophyta	42.2	56.8	*Aulocoseira granulata*
					Dinophyta	2.3	20.2	*Gymnodinium* sp.
					Cyanophyta	28.9	16.9	
					Euglenophyta	0.8	4.4	
					Chlorophyta	25.8	1.7	
			Total abundance (10^3 cells/m^2)	**Total biomass (g/m^2)**				
Phytobenthos	09 June 2010	33	1,328,238	2.251	Bacillariophyta	79.8	90.9	*Aulocoseira granulate*
					Chlorophyta	16.2	5.4	*Aulocoseira ambigua*
					Euglenophyta	1.6	3.6	*Amphora ovalis*
					Cyanophyta	2.4	0.06	
	16 June 2010	19	1,341,985	0.734	Bacillariophyta	27.4	85.7	*Aulocoseira granulata*
					Chlorophyta	28.1	14.3	
					Cyanophyta	44.5	0.04	

Discussion

The FA compositions of bivalve mollusk species significantly differed from those of their potential food sources of seston and sediments. Many authors revealed that FA compositions of animals do not completely reflect the FA compositions of the foods consumed. Along with trophic factors, phylogenetic factors are important determinants of FA profiles in aquatic invertebrates (Kraffe et al. 2008; Makhutova et al. 2011; Lau et al. 2012). Some invertebrates possess active elongases and desaturases and can significantly modify dietary FAs (Bell and Tocher 2009; Kelly and Scheibling 2012). Essential

Table 4 Abundance, biomass, and taxonomic composition of zooplankton and zoobenthos from Kanevskoe Reservoir, Ukraine

	Date	Number	Total abundance (individuals/L)	Total biomass (mg/L)	Dominant species	Percent total biomass
Zooplankton	9 June 2010	32	56.270	0.496	*Dreissena*, Veliger	42.6
					Cyclopoida juv., Copepoda	30.7
			Total abundance (individuals/m^2)	**Total biomass (g/m^2)**		
Zoobenthos	16 June 2010					
Unionidae		3	21.7	972.4	*Unio tumidus*	17.8
					Unio pictorum	16.4
					Anodonta anatina	16.6
Dreissenidae		2	1147.3	517.76	*Dreissena polymorpha*	37.1
					Dreissena bugensis	0.2
Others		27	596.3	165.72	*Viviparus viviparous*	
					Bithynia tentaculata	95.09[a]
					Theodoxus fluviatilis	2.37[a]
					Lithoglyphus naticoides	1.14[a]
					Dikerogammarus	0.58[a]
					Haemobaphes	0.44[a]

[a]Percent biomass of 'Others.'

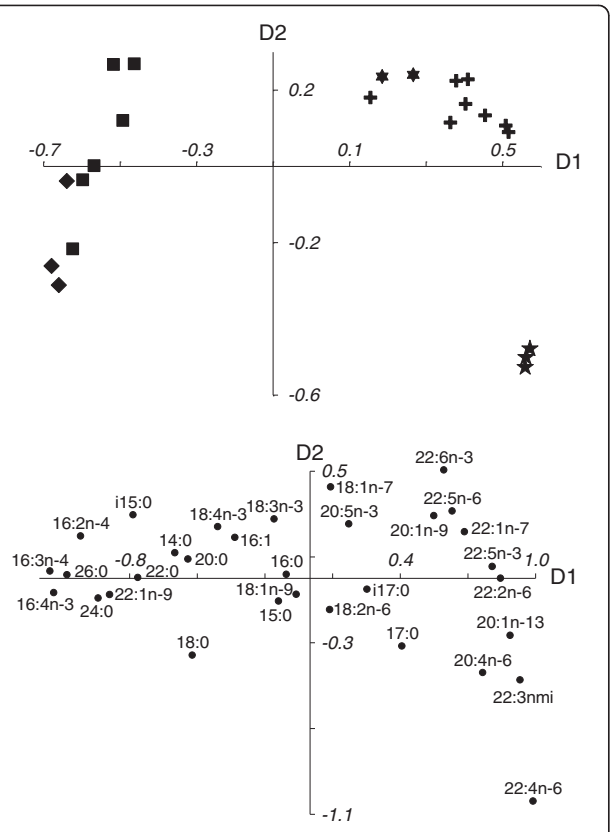

Figure 2 Canonical correspondence analysis of FA compositions of the mollusks, seston, and sediments from Kanevskoe Reservoir. Canonical correspondence analysis of the fatty acid (FA) composition (% of total FAs) of *Unio tumidus*, *Dreissena polymorpha*, *D. bugensis*, seston, and sediments from Kanevskoe Reservoir. Dimension 1 (D1) and dimension 2 (D2) represent 63.5% and 16.6% of the inertia, respectively. Squares, seston; diamonds, sediments; crosses, *D. polymorpha*; five-pointed star, *U. tumidus*; six-pointed star, *D. bugensis*.

dietary FAs, such as 18:2n-6 and 18:3n-3, can be used to synthesize physiologically important EPA and DHA that leads to decreased proportions of C18 PUFAs and increased proportions of C20 and C22 PUFAs in animal tissues compared to food items (Castell et al. 2004; De Troch et al. 2012). Long-chain PUFAs, such as EPA and DHA, are considered physiologically crucial and likely conservatively retained in tissues compared to other compounds (Gladyshev et al. 2011; Kelly and Scheibling 2012). In contrast, some other FAs, including FA markers of algae, are used as energetic resources and are catabolized in animal tissues (Brett et al. 2006; Gladyshev et al. 2011).

Seston and sediments also differed in percentages of several FA markers, showing higher input of decomposed material in sediments and a significant part of active phytoplankton, zooplankton, and bacterioplankton in seston. Although dominating taxa of the phytoplankton and phytobenthos were diatoms and dinoflagellates, FA markers of these algae were not abundant in seston and especially in sediments. The relatively low proportion of algal biomass in the seston is a possible reason for this result. High percentages of SFAs (18:0 and 20:0 to 26:0) and bacterial FAs in sediments and seston indicated a high proportion of detrital particles that may have comprised vascular plant detritus and also pseudofeces, feces, and other excreta of mollusks. Thus, in general, the contributions of algae to seston and especially to sediments were not high.

Differences in FA percentages of *Unio* and *Dreissena* species are apparently associated with differences in food sources of the mollusks. *Dreissena* likely preferred plankton species, while *Unio* probably consumed more detritus and benthic species. In addition to the high percentage of the detritus marker and relatively low levels of algae markers in *Unio*, NMI FAs may also indicate the preferred consumption of detritus by *Unio*. It is known that the unusual unsaturated pattern of NMI FAs confers a higher resistance to oxidative processes and microbial lipases on cell membranes than do common PUFAs (Irazù et al. 1984; Barnathan 2009). Thus, a high level of NMI FAs is considered a biochemical adaptation of benthic animals to their specific habitats (Barnathan 2009). In addition, some authors related NMI FA biosynthesis in mollusks to deficiencies in the physiologically important n-3 PUFAs, EPA, and DHA (Pirini et al. 2007). Both the sediments studied and *Unio* tissues were poor in EPA and DHA, and *Unio* feeding on benthic species may synthesize NMI FAs to compensate for the PUFA dietary deficiency.

As reported in the literature, bacteria can be a significant source of organic carbon and nitrogen for some bivalve mollusks (Nichols and Garling 2000). *Unio* and *Dreissena* studied in the present paper apparently consumed bacteria. It is well known that bacteria taxa markedly differ in FA markers or ratios (Bertone et al. 1996; Napolitano 1999; Saliot et al. 2001). When *Unio* was compared to both *Dreissena* species, it had significantly higher percentages of bacterial i17:0 and 17:0, which are likely markers of sulfate-reducing bacteria (Napolitano 1999). Hence, *Unio* might consume these bacteria together with detritus from sediments. In turn, percentages of another bacterial acid, 18:1n-7, which is abundant in cyanobacteria, and sulfur-oxidizing and aerobic bacteria (Napolitano 1999), were particularly high in both *Dreissena* species and seston samples. It is likely that *Dreissena* mostly consumed planktonic bacterial species.

Percentages of FA markers of green algae and cyanobacteria in mollusks and their food items were not high, due to the low biomass of Cyanophyta and Chlorophyta in the phytoplankton and phytobenthos. However, all of the mollusks studied probably consumed these algae. The percentage of 18:2n-6, the essential acid synthesized

by algae (Gugger et al. 2002; Caramujo et al. 2008), was higher in *Unio* than in either *Dreissena* species. Apparently, *Unio* consumed some algal species which contained this acid or selectively accumulated 18:2n-6 from its food. These data confirmed the selective feeding by bivalve mollusks as was reported by many authors (Dionisio Pires et al. 2004; Naddafi et al. 2007; Vuorio et al. 2007). Percentages of the essential FAs, 18:3n-3 and 18:4n-3, were substantially higher in *D. bugensis*, than in *Unio* and *D. polymorpha*. In aquatic food webs, the former FA is synthesized by green algae, cyanobacteria, or macrophytes, while the latter is abundant in some algal taxa, such as dinoflagellates and cryptophytes (Desvilettes et al. 1997; Gugger et al. 2002; Caramujo et al. 2008). *D. bugensis* may accumulate them from algal food sources that are rich in 18:3n-3 and 18:4n-3, or selectively assimilates them in contrast to other FAs. The source of 18:4n-3 could have been dinoflagellates that were the dominant species of phytoplankton (Table 3). DHA, another marker of dinoflagellates, was found in seston and was also significant in *D. bugensis*. Alternatively, *D. bugensis* might not use C18 n-3 PUFAs for subsequent FA biosynthesis as effectively as *D. polymorpha*. Significantly lower percentages of long-chain PUFAs in *D. bugensis* compared to *D. polymorpha* possibly confirm this suggestion.

Bacillariophyta are one of the dominating groups among the phytoplankton and phytobenthos (Table 3). However, we detected only negligible amounts of C16 PUFAs of the n-1, n-4, and n-7 families, markers of diatoms, in the mollusks studied. It was shown that consumers store these FAs mainly as triacylglycerols (TAGs) and preferentially use them for catabolism (Gladyshev et al. 2011). The mollusk tissues studied were poor in TAGs (our unpublished data), and hence, we cannot estimate the consumption of diatoms by mollusks using C16 PUFA markers. In addition to the above-mentioned C16 PUFAs, EPA and 16:1n-7 are also considered markers of diatoms (Table 1). *Dreissena* species had significant amounts of 20:5n-3 and 16:1 (mostly 16:1n-7), compared to *Unio*. Thus, we presumed that the consumption of diatoms by *Dreissena* species was higher than by *Unio*.

FA markers of vascular plant detritus may also be preferentially stored as TAGs. They were abundant in the seston and sediments, but insignificant in mollusks.

Zooplankton can also be a potential food source for mollusks. Copepods and veligers of *Dreissena* are dominant zooplankton species in the reservoir studied (Table 4), and their sizes were >0.2 mm. Particles of this size are too big and likely inedible by the studied species, especially *Dreissena*. Rotifers are of a suitable size, but their abundance and biomass were low. The high percentage of 22:1n-9, an FA marker of copepods (Table 1), in the seston and sediments, and low percentage of this acid in mollusks also indicated that mollusks did not feed on copepods. However, we did not take into account heterotrophic flagellates and ciliates as potential food items, which might be the sources of 18:2n-6, 20:4n-6, and 22:6n-3.

Thus, according to the FA marker analyses, *Dreissena* species and *Unio* had the following differences in feeding spectra. *Dreissena* preferred planktonic algae and bacteria, while *Unio* mostly consumed detritus and phytobenthic species. These results are in agreement with those of Cole and Solomon (2012) that *D. polymorpha* preferred phytoplankton compared to other food items. Furthermore, our results confirm the findings of Nichols and Garling (2000) that the main food source of unionids is detritus enriched with bacteria.

In addition to selective feeding, other factors could have caused differences in the feeding spectra of *Unio* and *Dreissena*. *Dreissena*, which settled on *Unio* shells, had a higher location compare to the fouled *Unio*. Hence, there was a higher availability of sestonic food items for *Dreissena*, while there was a higher availability of food items from sediments for *Unio*. Possible differences in particle sizes consumed by mollusks also might affect rations of mollusk species. As is known, dreissenids and unionids filter particles of a broad size range, including colonial and filamentous algae (Dionisio Pires et al. 2004; Bontes et al. 2007; Vanderploeg et al. 2009). The preferred sizes for *Dreissena* and *Unio* were similar and varied by up to 250 μm (Nichols and Garling 2000; Christian et al. 2004; Vaughn et al. 2008). This range includes sizes of almost all algal and bacterial species in the reservoir studied. Thus, all mollusks inhabiting Kanevskoe Reservoir ingested particles of the same range; consequently, the size of food particles was unlikely the reason for differences in the feeding spectra of these mollusks.

Unio and *Dreissena* species probably had significant differences in FA biosynthesis, since their percentages of n-6 and n-3 PUFAs, NMI FAs, and 20:1n-13 significantly differed. High percentages of n-3 PUFAs, especially EPA and DHA, in *Dreissena* species compared to *Unio* and food items probably indicate selective feeding and/or synthesis of these PUFAs by dreissenids from the essential precursors, C18 PUFAs. By contrast, *Unio* had significantly higher percentages of long-chain n-6 PUFAs, especially 20:4n-6 and 22:4n-6. These acids can be synthesized by *Unio* from dietary 18:2n-6 by Δ6 and Δ5 desaturases, which were detected in animals (Berge and Barnathan 2005; Kelly and Scheibling 2012). The mollusks studied, especially *Unio*, had a high level of 20:1n-13. Mollusks of different taxonomic positions and feeding spectra are known to contain a significant amount of this unusual isomer of 20:1 (e.g., Kawashima and Ohnishi 2004; Zhukova 2007; Saito and Hashimoto 2010; Kharlamenko et al. 2011). The method of biosynthesis of this FA is unclear. Some authors considered that 20:1n-13 is synthesized from 18:1n-13 by

C-2 elongation, whereas 18:1n-13 is derived from 18:0 by the action of Δ5 desaturase, generally common in bivalves (Saito and Osako 2007). However, some authors supposed that 20:1n-13 might be formed by a chain-shortening of 22:1n-13 which is itself formed by Δ9 desaturase acting on the 22:0 FA (Mansour et al. 2005). The role of 20:1n-13 in animals is unclear.

Conclusions

Our study demonstrated divergence in the feeding spectra of these mollusks (native populations of *U. tumidus* and invading populations of *Dreissena* species), which cohabitated and formed common druses. They obviously obtained foods of different qualities. *Dreissena* consumed plankton species, i.e., more-valuable food, while *Unio* fed on detritus and phytobenthic species which were of a lower food quality in terms of levels of physiologically important EPA and DHA. Under a deficiency of essential PUFAs, *Unio* synthesized specific FAs to compensate for the low food quality. We concluded that the different feeding spectra of mollusks and specific adaptations of *Unio* might be the basis for the successful coexistence of native species and invaders for a long time.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

AAP, ONM, MIG, and NNS conceived and designed the study. AAP, AAS, and IAM participated in the field trips for sampling and carried out hydrobiological analyses. ONM and GSK carried out biochemical analyses. MIG carried out statistical analyses and made the figures. ONM wrote the manuscript. MIG and NNS made intellectual contributions and reviewed the manuscript. All authors read and approved the final manuscript.

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