

Resource partitioning in endemic species of Baikal gastropods indicated by gut contents, stable isotopes and radular morphology

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Abstract We used multiple analytical methods to demonstrate resource partitioning in five species of coexisting endemic gastropods in the family Baicaliidae and the genus *Megalovalvata* (Valvatidae) in rocky walls of the underwater canyons in Lake Baikal. We tested whether filter-feeding baicaliids and valvatids consume and assimilate different food

using data from gut contents, stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes and radular morphology, with subsequent combined analyses. Our results showed that the four baicaliid species assimilate microalgae, diatoms and bacteria, whereas the single *Megalovalvata* species mostly assimilates plant detritus. The $\delta^{15}\text{N}$ variations in the baicaliids reflect differences in their digestion of seston components, whereas the $\delta^{13}\text{C}$ similarity illustrates consumption of food particles derived from similar primary producers. Gut contents in the baicaliids were dominated by a single species of planktonic diatom, although more than 30 species of microalgae were recorded in all seasons. However, the composition and quantity of additional food particles varied by species. Our results showed that baicaliids have significant fine scale differences in radular tooth morphology, which may allow partitioning of food resources.

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Introduction

The elevated endemism in Lake Baikal, Siberia, presents a model system for understanding questions of ecological coexistence and evolutionary divergence. Gastropods, like many groups here, are dominated by endemics in the lake with over 100 endemic lacustrine species among the 180 species

found in Baikal and adjacent water bodies. Past work has suggested that these species flocks are the result of adaptive radiation in different habitats of the shallow and deep water zones of the lake (Kozhov, 1936; Starobogatov & Sitnikova, 1990), but further data on their ecology will allow refinement of our perspectives on their divergence. Molluscs are ecologically important and diverse in this system. For example, the rocky walls of underwater canyons can be carpeted with baicaliids and valvatid snails, with 50,000 individuals per m² and biomass up to 1 kg per m² from 13 species (Fig. 1; Kamaltynov et al., 1998). Coexistence is common; more than 20 gastropod species have been recorded at a sandy habitat site (Lindholm, 1909; Kozhov, 1936; Sitnikova et al., 2010). It is axiomatic that these coexisting gastropods require sufficient amounts of food; an enquiry into ecological dynamics is critical for understanding how this system functions.

We address the question of trophic coexistence for five species of endemic gastropods in the family Baicaliidae and the genus *Megalovalvata* (Valvatidae) that live on hard substrate in an underwater canyon in Lake Baikal. Röpstorff et al. (2003) demonstrated that baicaliids are filter-feeders with stomach contents dominated by planktonic diatoms, mostly of a single common species. They showed that the taenioglossan radulae in baicaliids are relatively small (600 µm to 1.1 mm in seven investigated species) with similar gross morphologies among species. Valvatids graze on epiphytic algae and detritus in nutrient-rich habitats, but also filter feed on suspended organic matter, including microalgae and diatoms (Tsykhon-Lukanina, 1987).

Correlation between radular morphology and trophic differentiation has been reported both in sympatry and allopatry in gastropods. Coexisting rocky substrate species in marine and freshwater have been shown to have differences in radulae (Hawkins et al., 1989; Padilla et al., 1996; Reid & Mak, 1999; Jorgensen, 2001). Closely related taxa in tropical ancient lakes that live on different substrates have differences in radulae and isotopes that indicate that trophic divergence has played an important role in adaptive radiation in these systems (Michel, 2000; von Rintelen et al., 2004; Glaubrecht & Rintelen, 2008).

Carbon and nitrogen stable isotope ratios (¹³C/¹²C and ¹⁵N/¹⁴N) in hydrobiont tissues have been increasingly used to investigate feeding relationships in

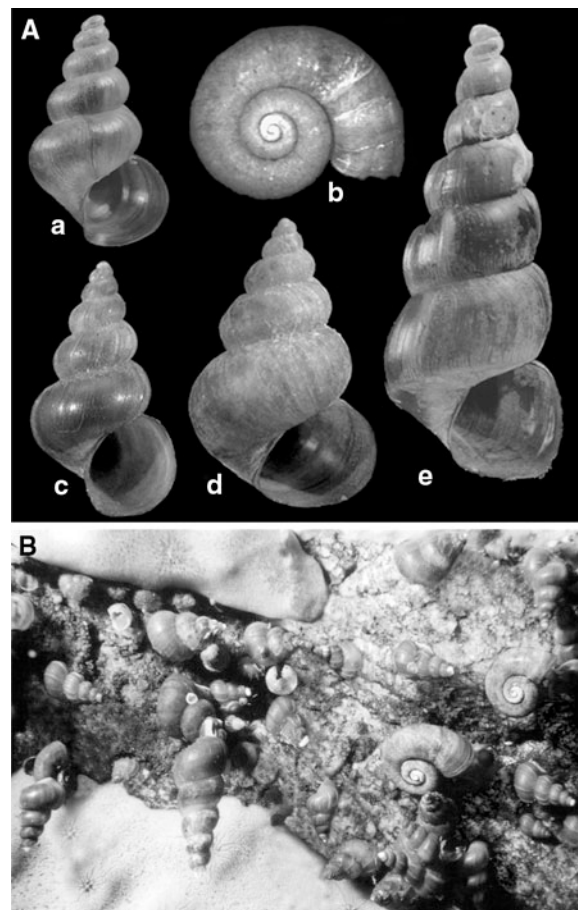


Fig. 1 **A** Shells of focal species (**Aa**) *Maackia herderiana* (shell height = 7.9 mm) (**Ab**) *Megalovalvata baicalensis* (shell diameter 12.3 mm) (**Ac**) *Maackia costata* (shell height = 9.2 mm) (**Ad**) *Teratobaikalia ciliata* (shell height = 9.6 mm) (**Ae**) *Baicalia turiformis* (shell height = 15.3 mm). **B** Habitat of the snails—canyon wall at 15 m in Lake Baikal (photo by O. Timoshkin)

freshwater and marine ecosystems (Yoshioka et al., 1994; Thompson et al., 2005; Cabanellas-Reboredo et al., 2009; Doi et al., 2010). The isotopic composition of organic matter in producers (autotrophs) depends on the composition of assimilated inorganic substances and metabolic pathways in such a way that all biogenic material has a particular “isotopic portrait” (Wada et al., 1993). Subsequent transformation of organic matter along the food chain leads heterotrophic organisms to inherit the isotopic composition of the producers and modify this to a unique signature of their own (DeNiro & Epstein, 1978; Minagawa & Wada, 1984). This makes it possible to use ¹³C/¹²C and ¹⁵N/¹⁴N ratios in tissues as natural

isotopic labels to indicate the source of consumed foodstuffs and position in the food web. In Lake Baikal, phytoplankton and primary benthic producers differ markedly by the content of ^{13}C isotope (Kiyashko et al., 1991, 1998; Yoshii et al., 1999), which enables identification of principal food sources for littoral animals. Regular enrichment of consumers by heavy isotopes along the food chain in Baikal ecosystem is reported to be 1.2 and 3.3‰ at each trophic level, for carbon and nitrogen, respectively (Yoshii et al., 1999). Isotope ratios are conservative indices reflecting composition of the food assimilated over a long-time period, whereas stomach contents reveal a snapshot indication of what food particles have been ingested.

In this study, we tested for fine-scaled partitioning of food resources between sympatric gastropods with two focal questions:

- (1) Are there significant dietary differences revealed by (a) gut contents and (b) carbon and nitrogen isotope ratios?
- (2) Are there differences in radular teeth that provide a mechanism for explaining any dietary differences?

Materials and methods

Sites and collections

Specimens were collected from rocky underwater canyons of two sites on the south-western shore of Lake Baikal: near Bolshie Koty Biological Station of Irkutsk State University (51°53' N, 105°03' E) and Listvenichnyi Bay (51°51' N, 104°53' E). SCUBA divers collected all snails on about 0.04 m² of rocky surface with a lift net. Samples included specimens of four baicaliid species, *Baicalia turriiformis* (W. Dybowski, 1875), *Maackia (Eubaicalia) herderiana* (Lindholm, 1909), *M. (M.) costata* (W. Dybowski, 1875) and *Teratobaikalia (Trichiobaikalia) ciliata* (W. Dybowski, 1875) and one valvatid, *Megalovalvata baicalensis* (Gerstfeldt, 1859). These five species comprise the numerical and biomass majority of 13 species inhabiting the rocky walls of Baikal canyons. Only adult snails were used for all analyses.

Stable isotope analyses were done on 10–15 randomly selected individuals of each species

collected on June 10, 1999 from 15 m at Bolshie Koty. Snails were placed in separate vessels with filtered lake water and delivered to the laboratory 1.5–2 h after they had been sampled. These samples included supporting data from gut content analyses on a selection of the same individuals.

More detailed stomach content analyses were done on samples collected in Listvenichnyi Bay from 15 m depth in September, 1999 (baicaliid species with exception of *M. herderiana*), in March, 2000 (with exception of *M. herderiana*), in May, 2000 (with exception of *T. ciliata*), in June, 2000 (all of four baicaliid species) and August, 2000 (only *B. turriiformis* and *M. herderiana*). Morphological studies of baicaliids were performed on samples collected in August–September, 2002 and June, 2007, also from Listvenichnyi Bay from 15 m depth.

Samples of valvatids for gut content and morphological analyses were collected in August, 2000 from 16 m depth in Listvenichnyi Bay. Samples were fixed immediately after collection in 4% formaldehyde for gut contents and in 80% alcohol for morphometrics.

Gut content methods

Food particles were quantified in five specimens of each species. After crushing the shell, each snail was dissected in distilled water. Food particles were removed from the stomach with a micropipette. Individual stomach contents were suspended in Karion A solution and mounted on a slide with a 18 × 18 mm cover slip for light microscopic examination at 320× to 16,000× magnification. Food particles were identified and each component larger than 10 μm was counted, according to a conventional method of phytoplankton and microphytobenthos analysis (Batterbee, 1986). Microalgae species identification was done by using Foged et al. (1993) and Lange-Bertalot & Genkal (1999). The average number of each dominant component in the gut was plotted by species as proportion of total particles. Minor gut components were quantified but are not presented graphically. Bacteria, rotatoria, protists, and diatoms containing green chloroplast were not counted but noted for presence-absence.

Isotope methods

Samples destined for isotope analysis were identified, the shell measured and removed, the animal sexed,

foot tissue cut off and the stomach dissected out in distilled water. Gut content analyses on these specimens were not as detailed as those described above, as only dominant microalgal species were recorded in a selection of individuals.

Foot tissue samples were dried at 60°C over 2 days and used for stable carbon isotope ratio analysis (SIRA). The foot is the most representative and conservative tissue for characterizing isotopic composition in molluscs (McKinney et al., 1999). Foot tissue is lipid poor, thus no lipid extraction was required. Carbon and nitrogen stable isotope ratios and C/N values were determined in powdered samples of about 1 mg weight using an EA 1108 elemental analyzer coupled via ConFlo II interface with a Finnigan MAT Delta-S mass-spectrometer in the Center for Ecological Research of Kyoto University. Isotope ratios are expressed by a conventional δ notation:

$$\delta X(\text{‰}) = \left[\left(R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right] \times 10^3,$$

where X is ^{13}C or ^{15}N , and R - $^{13}\text{C}/^{12}\text{C}$ or $^{14}\text{N}/^{15}\text{N}$, respectively. The PDB (PeeDee Belemnite) carbonate and atmospheric nitrogen were used as standards for carbon and nitrogen, respectively. Reproducibility of repeated analyses of gastropod tissues was better than $\pm 0.1\text{‰}$. For comparative context, we used data of Kiyashko et al. (1998) and Yoshii (1999) on carbon and nitrogen isotopes in the Lake Baikal littoral.

Radula methods

To control for size-related differences in radulae we took basic morphometric measures for the shell (height, width and length, width of aperture) and number of gill leaflets and gill length for each species. In baicaliids, the gill helps advance food through the mantle cavity (Röpstorff et al., 2003), thus is potentially related to both overall animal size and feeding efficiency. The shells were photographed and main shell variables measured using of Image-Pro Plus software package. The number of gill leaflets and gill length were calculated after the tissue dissection under light microscope. Radulae extracted from buccal mass of these specimens were cleaned with domestic bleach, rinsed several times with distilled water, dried and mounted onto SEM stubs. The radular teeth and cusps were examined and

measured using a Philips 525 Scanning Electron Microscope and measurements made with Image-Pro Plus. Variables were collected on height and width of the rachidian, the lateral and inner marginal teeth, height/width of cusps of these teeth and number of cusps per tooth (Fig. 4). Sample sizes for each component of this study are provided in Tables 3 and 4.

Statistical and analytical methods

Normality of each species $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data was confirmed with Kolmogorov–Smirnov tests before statistical analyses. Because all data sets fit assumptions of normality, one-way ANOVA was used to compare species, and Tukey HSD test was used to determine significant differences between species. Morphological data were subjected to t tests, correlation analyses and discriminant analyses. Discriminant analysis revealed which radula variables distinguished best among species. These confirmed that each specimen did indeed belong to one of the species under study. Statistical analyses were performed using STATISTICA-6 software package.

Results

Gut contents

Our results showed that gut contents for each focal species of baicaliid changed during the year, with differences among species in what they consumed, although 40 to 86% of food particles were consistent among sympatric species.

The size of microalgae found in stomachs varied from 1.5 to 200 μm (Table 1). Crushed diatom shells and sponge spicules were present in the guts, but their proportion to intact components was not recorded. Diatoms of genera *Cyclotella* and *Aulacoseira* are usually found in snail stomachs as separated cells whereas in nature they grow in ribbon-like colonies.

In June, 1999, planktonic diatoms containing green chloroplasts dominated the stomach contents of all five sampled species. In decreasing order of their abundance these were *Cyclotella minuta*, *C. baicalensis* and *Aulacoseira baicalensis*. The chlorophyte *Koliella longiseta* was also found. Valvate gut contents additionally included sponge

Table 1 Species list of microalgae occurring in Baikal gastropod guts, including habitat characteristics and taxonomic affiliation

	Species of microalgae	Character	Size of cells min.–max. (µm)
1	<i>Lyngbya limnetica</i> Lemm.	nbB	1.5–2
2	<i>Dinobryon cylindricum</i> Imhof.	pChr	40–56
3	<i>Gymnodinium baicalense</i> var. <i>minor</i> Antipova	pB	30–45
4	<i>Peridinium</i> sp.	pD	15
5	<i>Stephanodiscus</i> sp.	pB	4–6
6	<i>Aulacoseira baicalensis</i> (K. Meyer) Simonsen	pB	10 to 36–60
7	<i>A. islandica</i> (O.Müller) Simonsen	pB	10 to 20–30
8	<i>Synedra acus</i> Kütz.	pB	56–200 ^a
9	<i>Cyclotella baicalensis</i> Skv., Meyer	pB	40–150 ^a
10	<i>C. minuta</i> (Skv.) Antipova	pB	5–15
11	<i>Amphora ovalis</i> var. <i>affinis</i> Ehrb.	bB	34–50
12	<i>Achnanthes lanceolata</i> (Breb.) Grun.	bB	10–30
13	<i>Cocconeis placentula</i> Ehr. var. <i>placentula</i>	bB	20–50
14	<i>Cymbella ventricosa</i> var. <i>ventricosa</i> Bréb.	bB	14–28
15	<i>Didymosphenia</i> sp.	bB	40–65
16	<i>Didymosphenia geminata</i> (Lyngb.) M.	bB	48–135
17	<i>Eunotia polydentula</i> (Brun.) Hustedt	bB	10–30
18	<i>Fragilaria capucina</i> f. <i>lanceolata-baikali</i> Flower & Williams	nbB	46–86
19	<i>Gomphonema ventricosum</i> Greg.	bB	20–48
20	<i>G. quadripunctatum</i> (Østr.) Wisl.	bB	97–120 ^a
21	<i>G. acuminatum</i> (Kütz.) Rabenh.	bB	25–48
22	<i>Navicula cryptocephala</i> var. <i>cryptocephala</i> Kütz.	bB	20–36
23	<i>N. radiosa</i> Kütz.	bB	32–36
24	<i>N. tripunctata</i> (O. Müller) Bory	bB	45–60
25	<i>N. oppugnata</i> Hust.	bB	30–60
26	<i>Nitzschia dissipata</i> (Kütz.) Grun.	bB	24–60
27	<i>Rhoicosphenia curvata</i> (Kütz.) Grun.	bB	12–40
28	<i>Hannaea baicalensis</i> Genkal, Popovskaya, Kulikovskiy	bB	70–200 ^a
29	<i>Monoraphidium arcuatum</i> (Korsch.) Hind.	pChl	20
30	<i>Koliella longiseta</i> (Vischer) Hind.	pChl	30–40
31	<i>Chlorella</i> sp.	bChl	

b benthic, *nb* nectobenthic, *p* planktonic, *B* Bacillariophyta, *Chr* Chrysophyta, *Chl* Chlorophyta, *D* Dinophyta (size of the found cells is original no published data of G. Pomazkina)

^a Corresponded to maximum size of the cells living in Baikal water

spicules, plant detritus and organic matter of uncertain origin. The total species composition and exact quantity of all food particles were not calculated.

In September, 1999, gut contents were sampled from three sympatric baicaliid species, with major components shown in Fig. 2. The major gut components of *B. turriiformis* and *T. ciliata*, were roughly similar, and comprised mainly of Chrysophyceae cysts (55 and 42% of total food particles, respectively),

with the planktonic diatom *C. minuta* as the next most common component (39 and 31% of total food particles, respectively). However, the composition of additional components differed between these two species. *B. turriiformis* consumed three additional species of planktonic diatoms and a benthic diatom species, *Cocconeis placentula*. The food of *T. ciliata* was more diverse and consisted of six species of benthic diatoms and five species of planktonic

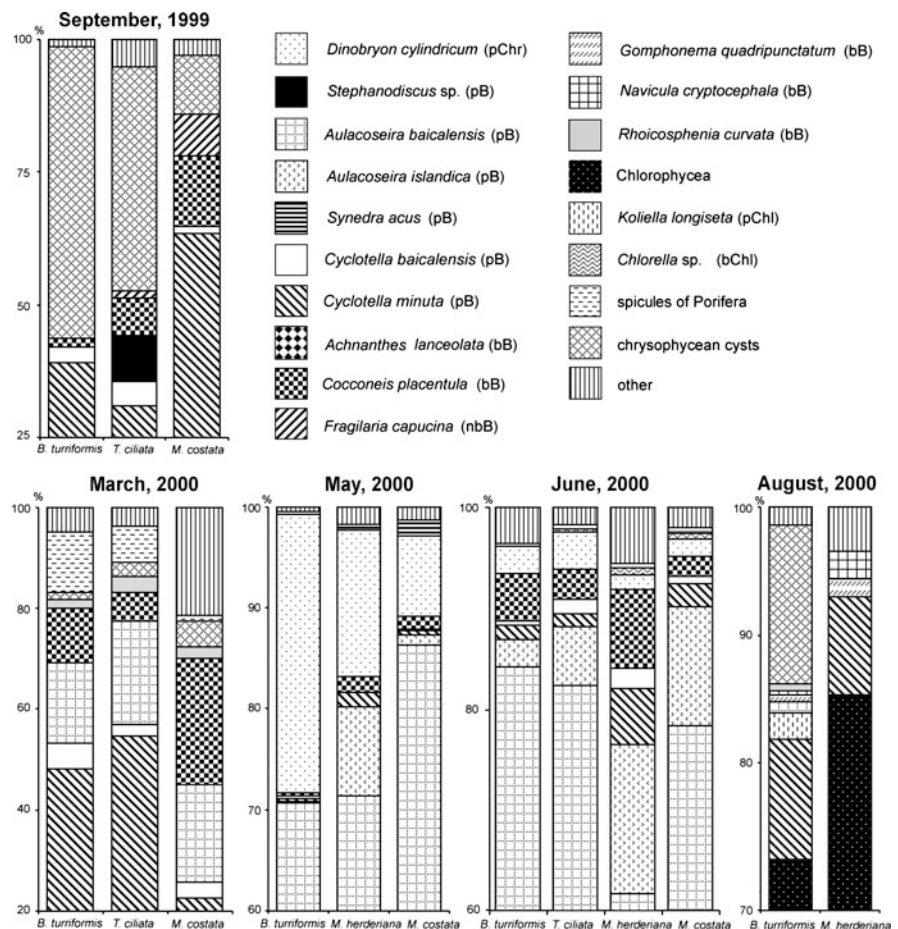
diatoms, all of which were absent in *B. turriiformis*. Gut contents of *M. costata* from the same sample contained seven species of benthic and two species of planktonic diatoms, dominated by *C. minuta* (63%). Gut contents also contained bacteria and sponge spicules, although these were not quantified in this sample.

In March, 2000, the same three species were sampled. *T. ciliata* and *B. turriiformis* had roughly similar gut contents; in both snails the planktonic diatom *C. minuta* dominated the total food particles (61 and 48%, respectively, Fig. 2). In *M. costata*, *C. minuta* formed an insignificant component of the gut contents which were dominated by benthic diatoms (51%), especially *C. placentula*. In *T. ciliata*, four of 11 total diatom species were planktonic, in *B. turriiformis* three of ten and in *M. costata* five of 22 species of diatoms. Sponge spicules and Chrysophyceae were also found in the gut of three baicaliids.

In May, 2000, the stomach contents of three baicaliid species were compared *B. turriiformis*, *M. costata* and *M. herderiana*. For all three, the planktonic diatom *A. baicalensis*, comprised from 70–86% of the total particles (Fig. 2). The second most frequent food particle was planktonic chrysophycean *Dinobryon cylindricum*. Sixteen additional species of were recoded, but the composition differed among baicaliid species. In *B. turriiformis*, 9 species were recorded, 6 of them were planktonic; *M. costata*—11 species (8 planktonic); in *M. herderiana*—10 species (6 planktonic). Other components included pine pollen, bacteria, sponge spicules and additional diatom species in low abundance.

In June, 2000, gut contents of four baicaliid species, *B. turriiformis*, *T. ciliata*, *M. herderiana*, and *M. costata* were assessed. Twenty nine species of microalgae were found overall. As in the results from the spring, the dominant component was the

Fig. 2 The gut contents of sympatric baicaliids sampled in 1999–2000



planktonic *A. baicalensis*, which comprised from 62 to 86% of the total food particles (Fig. 2). Only seven of the remaining algal species were planktonic diatoms, with the rest of the component from benthic sources.

In August, 2000, *B. turriiformis* and *M. herderiana* guts were assayed. *B. turriiformis* gut contents were dominated by Chlorophyceae (72% of total, not identified to species). *M. herderiana* gut contents were similar with Chlorophyceae comprising 82% of the total. The food particles of planktonic diatom *C. minuta* was found in stomachs of the both snails, while other food components were different (Fig. 2). The ratio of benthic and planktonic diatoms was 6:1 in the gut of *M. herderiana*, whereas eight benthic and four planktonic species were found in the gut of *B. turriiformis*.

In August, 2000, the valvatiid *M. baicalensis* was also surveyed. Sponge spicules were the main food component (about 40%, data not shown). Intact diatoms (28%) were represented by both planktonic (four) and benthic (nine) species. The stomachs also contained plant detritus, appearing as clots of brown-green matter with fragments of diatoms, Chlorophyceae microalgae, infusorians, cysts of Chrysophyceae and pollen.

Stable isotope composition

The valvatiid and all baicalioid species diverged markedly in carbon isotope signatures. $\delta^{13}\text{C}$ for the valvatiid ranged from -20.87 to -17.44‰ , with high intraspecific variance of 3.4‰ , whereas baicalioids had very low $\delta^{13}\text{C}$ values from -27.53 to -25.45‰ with low intraspecific variance of 1‰ (Table 2; Fig. 3). Despite a restricted range of carbon isotope composition, differences among baicalioid species were significant (one-way ANOVA, $F = 11.84$, $P = 0.0000005$). Mean $\delta^{13}\text{C}$ values showed significant depletion from -26.28 to -27.00‰ among *M. herderiana*, *T. ciliata*, and *B. turriiformis* (Tukey HSD test, $P < 0.05$). The mean $\delta^{13}\text{C}$ value of *M. costata* was intermediate between those of *T. ciliata* and *B. turriiformis* and not significantly different from either of them (Table 2; Fig. 3).

Differences in mean $\delta^{15}\text{N}$ values among all species were statistically significant (Tukey HSD test, $P < 0.05$). The $\delta^{15}\text{N}$ ratios of individual snails ranged from as low as 4.98‰ for *M. herderiana* to as high as

7.55‰ for *M. baicalensis* (Table 2). Intraspecific variations in $\delta^{15}\text{N}$ were about 1‰ for all five species studied. There was no correlation between sex, shell size, C/N ratio, and $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ in the species under study.

Morphology

Both *Maackia* species, *M. herderiana* and *M. costata*, have an elongated conic shell shape with a small aperture size and similar sizes. Two other sympatric species differ in shell shape and size. *Teratobaicalia ciliata* has a broadly conic shell and wide aperture, whereas *B. turriiformis* has a large elongate shell with high spire (Fig. 1B; Table 3). The shells of all of these species have ribs or carinae of different strengths.

The radulae of baicalioids in this study were $645\text{--}1100\ \mu\text{m}$ long with $54\text{--}80$ rows of teeth and the valvatiid *M. baicalensis* had a radula about $1500\ \mu\text{m}$ long, with $23\text{--}27$ rows of teeth. The size of *M. baicalensis* radulae exceeded that of baicalioids about five times in tooth size and three to seven times in cusp size. The number of cusps per tooth, however, is almost equal (Table 4). A part of the radula ribbon with rachidian, lateral, and marginal teeth of *M. baicalensis* is illustrated in Fig. 4.

In gross morphology, radulae were indistinguishable among baicalioid species in this study (Fig. 5A–D, left column). Characters 5–9 (Table 3) indicate that radular dimensions differed only slightly and did not depend on the shell height and width ($r = -0.17\text{--}0.57$, $P > 0.01$). However, these data are preliminary as sample sizes were small.

Baicalioid species did differ quantitatively in tooth structure, especially in size and shape of the lateral teeth (Fig. 5Ab–Db). Multivariate discriminant function analyses of the size of the teeth and cusps (Table 4, characters 1, 2, 4, 5, 7; 8, 10, 11 and Table 5, all characters) revealed non-overlapping point clouds for each of the four species in three-dimensional multivariate canonical space (Fig. 6A). Five characters provided the separation: height of the rachidian, lateral and marginal teeth and height of cusps of the rachidian and marginal teeth. In addition of the number of cusps per tooth into the analysis uncovered two groups, one with *M. costata* and *T. ciliata* which has 4–10 cusps more on the rachidian and marginal teeth than the other group, with

Table 2 Carbon and nitrogen stable isotope ratios and C/N ratio of focal gastropods

Species (number of individual samples analyzed)	$\delta^{13}\text{C}$ (‰) mean \pm SD (range)	$\delta^{15}\text{N}$ (‰) mean \pm SD (range)	C/N mean \pm SD
<i>Baicalia turritiformis</i> (n = 15)	-27.00 ^a \pm 0.25 (-27.53 to -26.55)	5.67 \pm 0.31 (5.11 to 6.41)	4.08 ^b \pm 0.27
<i>Maackia costata</i> (n = 15)	-26.89 ^{ab} \pm 0.31 (-27.42 to -26.43)	6.14 \pm 0.43 (5.39 to 6.96)	4.39 ^a \pm 0.32
<i>Teratobaicalia ciliata</i> (n = 15)	-26.66 ^b \pm 0.34 (-27.37 to -26.06)	6.51 \pm 0.26 (5.99 to 6.88)	4.02 ^b \pm 0.30
<i>Maackia herderiana</i> (n = 13)	-26.28 \pm 0.47 (-27.17 to -25.45)	5.31 \pm 0.21 (4.98 to 5.67)	4.45 ^a \pm 0.23
<i>Megalovalvata baicalensis</i> (n = 10)	-19.66 \pm 1.19 (-20.87 to -17.44)	7.01 \pm 0.42 (6.49 to 7.55)	4.06 ^b \pm 0.15

Mean values marked by the same letter are not significantly different (one-way ANOVA Tukey HSD test, $P > 0.05$)

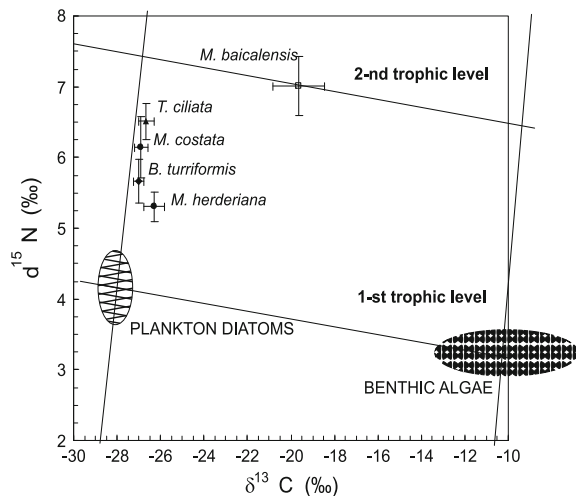


Fig. 3 Plot of the $\delta^{13}\text{C}$ and the $\delta^{15}\text{N}$ values (means and SD) of sympatric Baikal gastropods in an underwater canyon. Isotopic data on plankton diatoms and benthic algae are presented after Kiyashko et al. (1998), Yoshii (1999), Yoshii et al. (1999). Trophic levels are shown according to Yoshii et al. (1999)

M. herderiana and *B. turritiformis* (Fig. 6B; Table 4, characters 3, 6, 9, 12).

As with radulae, the external ctenidium of the valvatid species was markedly different from all the baicaliids, with 6–11 times fewer gill leaflets (Table 3, characters 10, 11). The ctenidium of the investigated baicaliids was composed of 78–120 triangular leaflets at the gill length of about from 6 to 13 mm. The gill of fixed valvatids was very small, about 2 mm of the length.

Among baicaliids variation in the ctenidium did not correlate with shell size at the species level

($r = -0.04-0.24$, $P > 0.05$). *M. herderiana* and *M. costata* were similar in shell size, but differed significantly in the number of leaflets ($t = 12.93$, $P < 0.0000$), whereas the largest species, *B. turritiformis*, had significantly fewer ($t = 5.39$, $P < 0.0000$) number of leaflets to the smallest species, *M. costata* (Table 3).

Discussion

Our combined results of gut contents, isotopes and radulae morphology indicate that the sympatric Baikal gastropods in this study partition their food resources on a fine scale. Detailed sampling of gut contents across a range of seasons and years was necessary, as it has been recognized that the algal flora of Baikal varies both annually and seasonally. We focused on five species of sympatric gastropods in our sampling, four baicaliids and one valvatid, but will discuss the results with reference to what is known about other gastropods from Lake Baikal as well.

Gut contents

The baicaliids in this study were all microphytophagous, occupying a similar herbivorous trophic level, though detailed analyses revealed species and temporal differences. Although their guts contained more than 30 species of microalgae, usually a single species dominated. Both the dominant and minor

Table 3 Shell, radulae and gill dimensions in five Baikal gastropod species (mean \pm SD/min.–max. and number of measurements is given in brackets)

Morphological characters	<i>M. costata</i>	<i>M. herderiana</i>	<i>T. ciliata</i>	<i>B. turriiformis</i>	<i>M. baicalensis</i>
1 Shell height (mm)	9.25 \pm 0.54	8.15 \pm 0.45	9.69 \pm 0.74	14.82 \pm 1.35	4.3 \pm 0.34
	8.1–10.0 (15)	7.5–9.4 (15)	8.6–11.0 (15)	12.9–16.9 (9)	3.9–4.8 (7)
2 Shell width (mm)	5.07 \pm 0.33	4.77 \pm 0.29	5.73 \pm 0.46	5.8 \pm 0.67	10.04 \pm 0.72
	4.2–5.0 (15)	4.3–5.3 (15)	5.0–6.0 (15)	5.0–6.9 (9)	9.1–11.0 (7)
3 Length of aperture (mm)	3.52 \pm 0.28	3.62 \pm 0.37	3.67 \pm 0.26	4.17 \pm 0.44	3.7 \pm 0.1
	3.2–3.8 (5)	3.1–4.1 (5)	3.3–3.9 (6)	3.5–4.7 (6)	3.6–3.8 (3)
4 Width of aperture (mm)	2.68 \pm 0.08	2.68 \pm 0.13	3.3 \pm 0.14	3.33 \pm 0.34	3.37 \pm 0.29
	2.6–2.8 (5)	2.6–2.9 (5)	3.1–3.5 (6)	3.0–3.8 (6)	3.2–3.7 (3)
5 Length of radula (μ m)	729 (1)	711 (1)	645 (1)	1100 (1)	1498 \pm 88
					1420–1620 (4)
6 Width of radula (μ m)	103 \pm 5	108 \pm 4	126 \pm 17	119 \pm 6	354 \pm 65
	93–108 (5)	104–113 (3)	100–137 (5)	112–128 (6)	273–450 (5)
7 No. of teeth rows	66 (1)	60 (1)	56 (1)	80 (1)	25 \pm 2
					23–27 (4)
8 Ratio of radula width to length of aperture (%)	2.95 \pm 0.26	3.00 \pm 0.49	3.44 \pm 0.49	2.81 \pm 0.29	7.82 \pm 0.35
	2.46–3.37 (25)	2.15–4.13 (20)	2.59–4.19 (30)	2.38–3.46 (24)	7.18–8.39 (12)
9 Ratio of length 5 rows to width of radula	0.69 \pm 0.04	0.7 \pm 0.05	0.69 \pm 0.05	0.79 \pm 0.04	0.92 \pm 0.07
	0.62–0.74 (5)	0.65–0.73 (3)	0.63–0.75 (5)	0.75–0.83 (6)	0.86–1.02 (4)
10 Length of gill (mm)	6.0–9.3 (3)	5.7–5.9 (3)	9.2–15 (5)	9.7–13.2 (3)	1.5–2.0 (3)
11 No. of gill leaflets	110 \pm 6	85 \pm 6	90 \pm 6	95 \pm 6	12 \pm 1
	102–120 (15)	78–95 (25)	83–104 (15)	90–118 (8)	11–14 (7)

components of the gut are likely to track the variation in available food resources, though notably there are differences among sympatric species. Different diatom species dominate in Baikal plankton in different years (Antipova, 1974; Bondarenko & Guselnikova, 1989; Kozhova & Izmet'seva, 1998). Evstafyev & Bondarenko (2007) showed that *C. minuta* dominated in 1999, whereas *A. baicalensis* did so in 2000. This was reflected in the dominant gut content components in our study.

After the presence of the most common microalgae, the remaining dietary components differed among baicalioid species, and changed through the year (Fig. 2). Microalgae in baicalioid stomachs had both planktonic and benthic origins. Eighteen of 31 identified species were benthic, two were nectobenthic and 11 were planktonic (Table 1). Karabanov & Fialkov (1987) suggest that the main food source for animals inhabiting rocky walls of the canyon is seston containing suspended biogenic and terrigenous material that is introduced from the shallow-water terrace by water currents. The phytoplankton in the littoral

zone of Baikal includes up to 80% microalgae species with benthic origin (Bondarenko & Logacheva, 2009). These data explain the presence of plankton as benthic and nectobenthic microalgae and diatoms as well as sponge spicules in the guts of the filter-feeding littoral gastropods surveyed in this study.

The mixed diet of benthic microalgae and coastal phytoplankton revealed in Baikal snails is not unique for molluscs, as it has been demonstrated in deposit-feeding Assimineidae (Kurata et al., 2001) and in the suspension-feeding bivalves (Yokoyama et al., 2009).

Our results for valvatids underscore the importance of examining species level differences in diet. Previous work on the diet of another Baikal endemic *Megalovalvata* species showed that *M. demersa* consumes benthic diatoms (periphyton) (Röpstorff et al., 2003). However, our results showed that the related *M. baicalensis* consumes mainly detritus from the surface of sponges. It is possible that the Baikal littoral valvatids have a mixed diet, but instead of benthic-planktonic composition observed in baicaliids their food consists of detritus and benthic diatoms.

Table 4 Measurements of radular teeth in five Baikal gastropod species (mean \pm SD/min. - max. and number of measured teeth is given in brackets)

Morphological characters	<i>M. costata</i>	<i>M. herderiana</i>	<i>T. ciliata</i>	<i>B. turriiformis</i>	<i>M. baicalensis</i>
1 Central tooth height (μm)	10.4 \pm 1.5 7.33–12.9 (21)	10.1 \pm 1.7 7.9–13.4 (16)	11.5 \pm 1.7 9.25–13.9 (15)	15.6 \pm 2.4 11.9–19.6 (26)	72.6 \pm 4.9 64.0–77.9 (10)
2 Central tooth width (μm)	15.29 \pm 1.6 11.8–17.3 (21)	12.6 \pm 1.2 11.1–14.7 (16)	18.6 \pm 2.4 14.8–21.7 (15)	20.3 \pm 3.1 15.6–26.7 (26)	81.1 \pm 4.7 72.9–89.9 (10)
3 No. of cusps of central tooth	32 \pm 3 27–36 (9)	25 \pm 2 21–29 (19)	29 \pm 3 25–34 (20)	25 \pm 3 22–30 (7)	33 \pm 4 27–39 (7)
4 Lateral tooth height (μm)	26.9 \pm 2.2 23.4–30.9 (10)	26.3 \pm 2.6 21.5–31.2 (14)	35.1 \pm 6.5 23.0–44.7 (12)	30.7 \pm 2.8 26.2–36.9 (14)	98.4 \pm 6.2 91.9–107.6 (10)
5 Lateral tooth width (μm)	18.3 \pm 1.05 16.6–20.0 (10)	21.5 \pm 1.7 18.4–24.3 (14)	22.0 \pm 3.0 18.4–26.0 (12)	21.6 \pm 2.5 18.1–26.2 (14)	58.6 \pm 5.6 50.8–68.2 (10)
6 No. of cusps of lateral tooth	35 \pm 2 32–37 (11)	41 \pm 4 34–45 (7)	33 \pm 2 30–37 (11)	35 \pm 2 32–38 (6)	36 \pm 5 31–43 (6)
7 First marginal tooth height (μm)	35.86 \pm 4.53 27.79–44.14 (18)	30.51 \pm 1.96 27.34–35.3(16)	48.97 \pm 5.02 33.89–57.1 (11)	40.01 \pm 4.03 35.64–47.74 (10)	133.59 \pm 16.53 113.1–161 (130)
8 First marginal tooth width (μm)	8.9 \pm 1.4 7.1–11.5 (18)	10.0 \pm 1.1 8.8–11.9 (16)	8.9 \pm 0.9 7.6–10.1 (11)	10.1 \pm 1.8 7.6–13.7 (10)	43.7 \pm 5.8 32.4–52.9 (13)
9 No. of cusps of 1-st marginal tooth	43 \pm 5 37–52 (6)	38 \pm 2 36–40 (6)	48 \pm 7 41–56 (6)	34 \pm 3 31–39 (9)	41 \pm 8 32–55 (10)
10 Second marginal tooth height (μm)	37.2 \pm 3.9 31.7–43.0 (17)	28.4 \pm 3.2 23.9–36.3 (16)	47.9 \pm 6.9 34.7–59.0 (17)	45.1 \pm 5.3 33.9–51.3 (11)	127.5 \pm 11.88 110.7–140.4 (10)
11 Second marginal tooth width (μm)	10.8 \pm 2.9 7.4–15.5 (17)	9.6 \pm 1.1 7.64–11.3(16)	8.6 \pm 1.4 6.9–11.7 (17)	8.6 \pm 1.2 6.6–10.4 (11)	43.6 \pm 2.9 39.4–46.9 (10)
12 No. of cusps of 2nd marginal tooth	33 \pm 2 31–35 (6)	23 \pm 2 20–24 (6)	30 \pm 8 24–44 (6)	24 \pm 4 21–28 (6)	38 \pm 3 35–41 (6)

A similar mixed diet has been indicated in sympatric planorbids *Anisus (Bathyomphalus) contortus* and *Anisus (Gyraulus) acronicus* in a northwest Siberian lake, which consume detritus in combination with algae (Arakelova and Michel, 2009).

Stable isotope composition

The species-level dietary differences shown in our gut content results were supported by the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ differences in snail body tissues. In Fig. 3, we compare the isotope composition of our focal gastropod species and the principal sources of organic matter in the littoral zone of Lake Baikal using published data (Kiyashko et al., 1998; Yoshii et al., 1999). Baikal phytoplankton, which is dominated by diatoms, is characterized by relatively constant isotopic composition with mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of -28.0 and 4.2‰ , respectively (Kiyashko et al., 1998; Yoshii

et al., 1999). Benthic macro- and microalgae, including periphytic diatoms, are characterized by much higher $\delta^{13}\text{C}$ values, from -14.0 to -5.0‰ (Kiyashko et al., 1998), although their average $\delta^{15}\text{N}$ 3.0‰ is similar to phytoplankton (Yoshii, 1999). Phytoplankton seems to be the primary carbon source for the four focal species of baicaliids, as indicated by the similarity in $\delta^{13}\text{C}$ values (Fig. 3). It should be noted that the majority of other previously investigated invertebrates (some caddis flies, amphipods and oligochaetes) inhabiting the exposed Baikal southwestern littoral have $\delta^{13}\text{C}$ values higher than -20‰ (Kiyashko et al., 1998), which is similar to our focal taxa. Only sponges and the filter-feeding polychaete *Manayunkia baicalensis* exhibited lower $\delta^{13}\text{C}$ values (under -25.0‰) than did baicaliid gastropods (Kiyashko et al., 1998; Yoshii, 1999).

Statistically significant differences in mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were found among our focal

Table 5 Measurements of the cusps of radular teeth (mean \pm SD/min.–max. in μm and number of measured cusps is given in brackets)

No	Radular teeth characters	<i>M. costata</i>	<i>M. herderiana</i>	<i>T. ciliata</i>	<i>B. turrimiformis</i>	<i>M. baicalensis</i>
1	Central cusp height of central tooth	2.3 \pm 0.3	2.6 \pm 0.1	3.8 \pm 0.3	3.5 (1)	18.1 \pm 2.1
		2.0–2.9 (5)	2.5–2.6 (4)	3.5–4.0 (3)		15.6–20.5 (5)
2	Central cusp width of central tooth	1.2 \pm 0.2	2.1 \pm 0.2	1.9 \pm 0.1	2.6 (1)	9.8 \pm 0.4
		1.0–1.4 (5)	1.9–2.2 (4)	1.8–2.1(3)		9.5–10.6 (5)
3	Lateral cusp height of central tooth	1.8 \pm 0.2	1.9 \pm 0.2	1.9 \pm 0.5	2.8 \pm 0.4	8.5 \pm 2.7
		1.2–2.2 (57)	1.5–2.3 (64)	0.9–3.2 (51)	1.9–3.5 (46)	3.1–12.8 (28)
4	Lateral cusp width of central tooth	0.45 \pm 0.1	0.6 \pm 0.2	0.5 \pm 0.2	0.8 \pm 0.2	3.2 \pm 1.1
		0.3–0.7 (57)	0.2–1.0 (64)	0.2–0.97(51)	0.4–1.3 (46)	1.3–5.4 (28)
5	Cusp height of lateral tooth	1.9 \pm 0.4	2.2 \pm 0.4	2.7 \pm 0.5	2.5 \pm 0.4	10.5 \pm 3.3
		1.2–1.7 (23)	1.7–3.2 (28)	2.1–3.9 (29)	1.7–3.5 (36)	7.3–20.8 (23)
6	Cusp width of lateral tooth	0.6 \pm 0.3	0.8 \pm 0.2	0.7 \pm 0.4	0.8 \pm 0.2	3.4 \pm 1.9
		0.3–1.3 (23)	0.5–1.3 (28)	0.3–2.2 (29)	0.5–1.2 (36)	7.3–20.8 (23)
7	Cusp height of first marginal tooth	1.4 \pm 0.3	1.8 \pm 0.3	2.2 \pm 0.5	1.9 \pm 0.3	8.3 \pm 2.8
		1.0–1.9 (31)	1.2–2.5 (58)	1.4–3.2 (22)	1.3–2.7 (32)	3.1–18.4 (89)
8	Cusp width of first marginal tooth	0.4 \pm 0.1	0.6 \pm 0.1	0.5 \pm 0.1	0.6 \pm 0.2	2.0 \pm 0.9
		0.2–0.7 (31)	0.4–0.9 (58)	0.4–0.6 (22)	0.3–1.1 (32)	1.1–6.4 (89)
9	Cusp height of second marginal tooth	1.4 \pm 0.2	1.7 \pm 0.2	2.1 \pm 0.3	1.7 \pm 0.1	7.6 \pm 4.9
		1.1–2.0 (31)	1.2–2.2 (44)	1.5–2.5 (27)	1.3–1.9 (17)	1.3–17.1 (50)
10	Cusp width of second marginal tooth	0.5 \pm 0.2	0.7 \pm 0.2	0.5 \pm 0.1	0.5 \pm 0.1	2.3 \pm 1.1
		0.2–1.0 (31)	0.3–1.0 (44)	0.3–0.7 (27)	0.3–0.7 (17)	0.8–7.4 (50)

gastropod species. Apart from differences in food source, differences in lipid content could have a significant effect on the $\delta^{13}\text{C}$ variations of organisms, because lipids are depleted in ^{13}C relative to other body components (Smyntek et al., 2007). Atomic C/N ratios are considered as a good proxy for lipid content to evaluate the effect of lipids on bulk tissue $\delta^{13}\text{C}$ (Post et al., 2007). Molluscan foot tissue samples studied were characterized by low lipid content and similar C/N ratios. We found no correlation between $\delta^{13}\text{C}$ and C/N values either for all samples analyzed or for individual gastropod species. Consequently, we concluded that inter-species differences in gastropod mean $\delta^{13}\text{C}$ values were not related to lipid content variations. All gastropods were collected for isotopic analysis at the same site and at the same time, thus we assumed that inter-species $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ differences among coexisting species are the result of different assimilation of various dietary components.

The body tissues of baicaliids were enriched in ^{15}N relative to planktonic diatoms by 1.1 to 2.3‰, i.e., far less than supposed for one trophic level (3.3‰, see

Yoshii et al., 1999). The lower ^{15}N -enrichment of baicaliids could be the result of assimilation of various amounts of nitrogen-fixing bacteria. For example, planktonic cyanobacteria in Baikal are characterized by low $\delta^{15}\text{N}$ values of about 2.7‰ (Yoshii et al., 1999). During different years, the autotrophic picoplankton of Lake Baikal included 10 to 90% of cyanobacteria depending on the development stage of diatoms (Bondarenko & Guselnikova, 1989; Popovskaya & Belykh, 2003; Belykh & Sorokovikova, 2003). Moreover, the $\delta^{15}\text{N}$ values in our focal baicaliids coexisting on rocky walls (Table 2) could be explained by consuming other components of seston that were not counted in this study, for example, bacteria. The earliest work on baicaliid diets (Rodina, 1951), based on microbiological analysis of gut contents, suggested that autotrophic and heterotrophic bacteria form the basic diet. Cultured Baikal cyanobacteria were successfully used as one of the food components for laboratory culture of *M. herderiana* (Maximova et al., 2007). It is possible that diets of the focal gastropods in this study change through ontogeny, as this has been demonstrated in Baikal acroloxids, the young of which

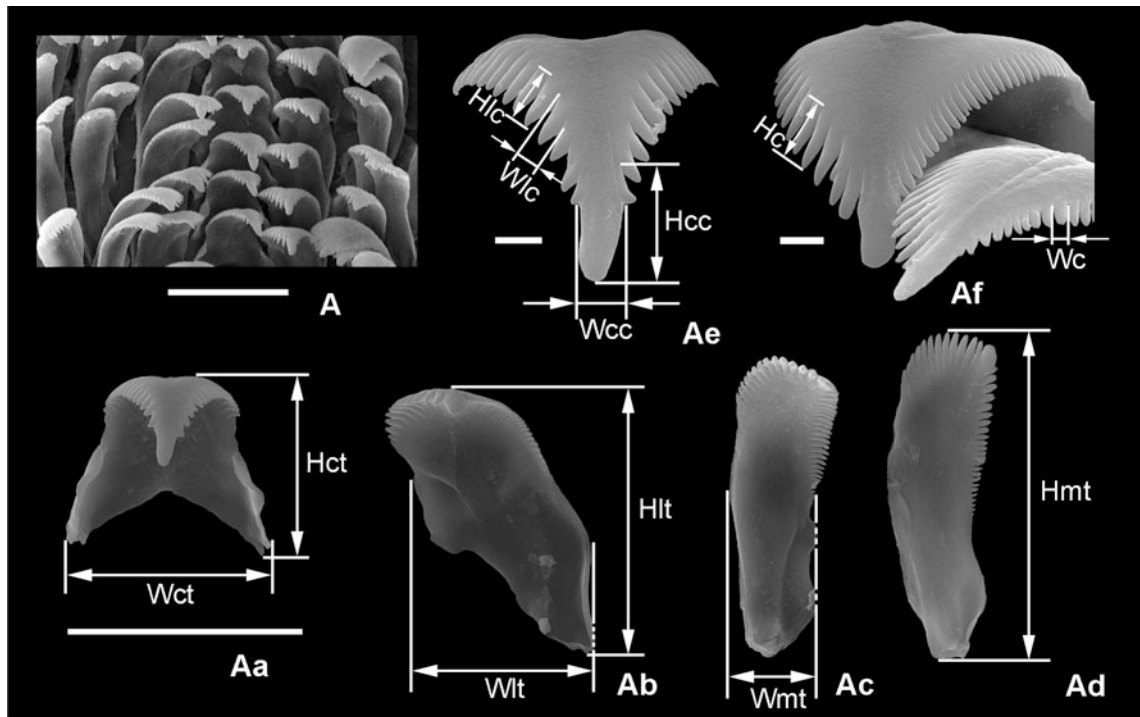


Fig. 4 Portion of the radula ribbon and teeth of *Megalovalvata baicalensis* with scheme of measurements. Scale bars: **A–Ad** = 0.1 mm, **Ae–Af** = 10 μ m. **Ae**, cusps of a rachidian tooth; **Af**, cusps of lateral and marginal teeth; **Hct**, height of a rachidian tooth; **Wct**, width of a rachidian tooth; **Hlt**, height of a lateral tooth; **Wlt**, width of a lateral tooth; **Hmt**, height of

marginal teeth; **Wmt**, width of marginal teeth; **Hcc**, height of a central cusp on rachidian tooth; **Wcc**, width of a central cusp of rachidian tooth; **Hlc**, height of lateral cusps of rachidian tooth; **Wlc**, width of lateral cusps of rachidian tooth; **Hc**, height of cusps of lateral and marginal teeth; **Wc**, width of cusps of lateral and marginal teeth

consume planktonic diatoms whereas the adults feed mainly the benthic microalgae (Shirokaya, 2003).

The valvatid *Megalovalvata baicalensis* is sympatric with baicaliids, yet contrasts strongly in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios (Table 2; Fig. 3). The estimated values of stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes of *M. baicalensis* indicate that it feeds mainly on plant detritus both of planktonic and benthic origin and which come from the seston as well as from sponge surfaces where this snail can be found and presumably grazes. Whether *M. baicalensis* consumes sponge tissue for nutritive value, or only incidentally, will be investigated in further research.

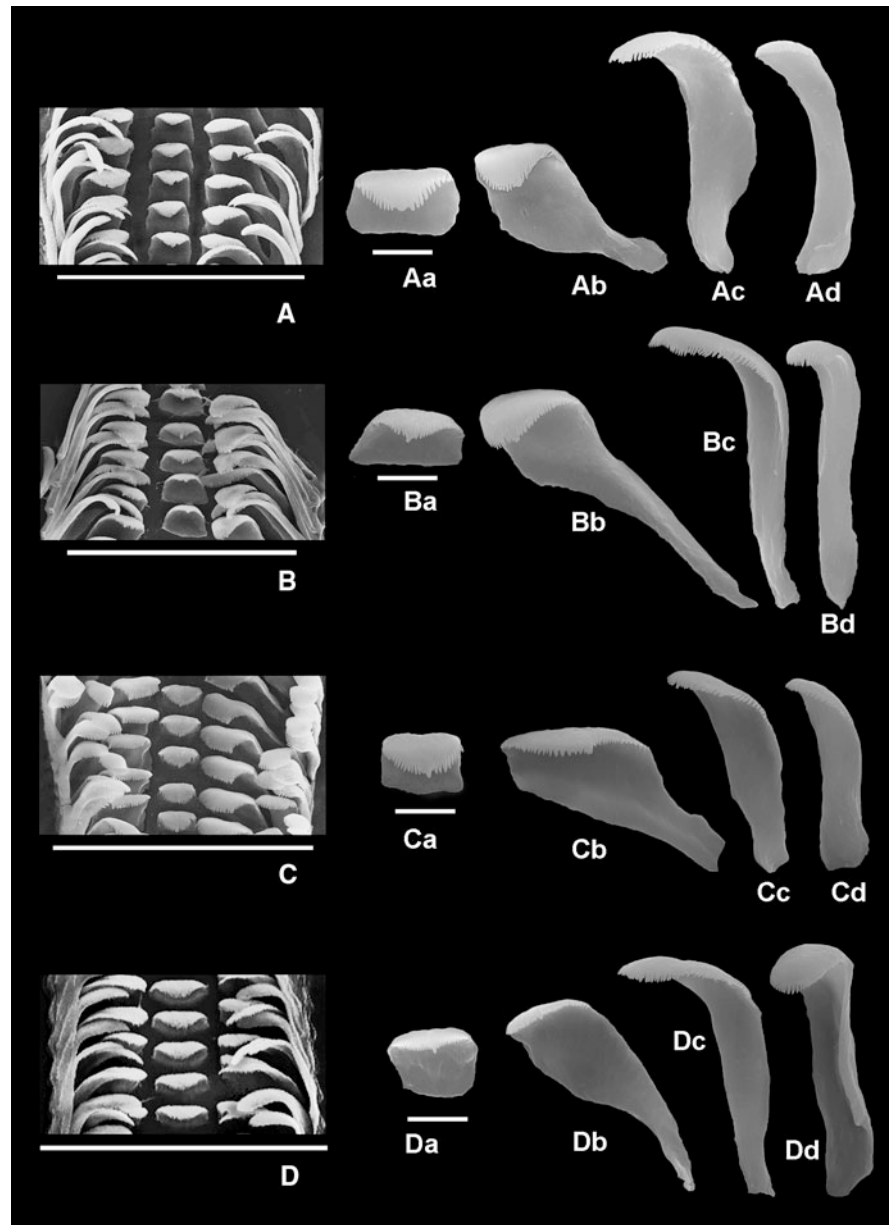
Significant $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ differences among sympatric Baikal baicaliids and valvatid species is compelling evidence of the complex utilization of food sources on rocky steep walls. Different food pathways have been revealed among invertebrates in other systems, in spite of similarities of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between some grazers and suspension-feeders, including among gastropods, associated with

Ascophyllum nodosum on rocky marine coast (Riera et al., 2009). Lack of significant differences between some pairs of sympatric baicaliids species in carbon stable isotopes is not unexpected. Similar values of $\delta^{13}\text{C}$ have been revealed between marine grazing snails *Littorina squalida* and *Homalopoma sanganense* which coexist on the seagrass *Zostera marina*; however, both species differ significantly from the surface deposit feeding gastropod *Batillaria cumingi* (Kharlamenko et al., 2001). It is interesting, two sympatric species of *Assiminea* found in salt marshes have carbon isotopes values that are comparable to the Baikal valvatid *M. baicalensis* at -20.7 ± 0.3 and -19.8 ± 0.5 ‰ (Kurata et al., 2001). These *Assiminea* consume mainly deposited organic matter.

Morphology

Differences in the size and shape of radular teeth have been recognized as taxonomic characters for baicaliids species (Dybowski, 1875; Kozhov, 1936),

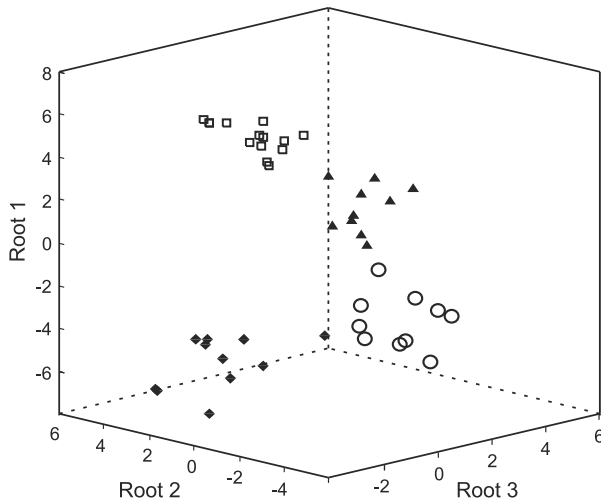
Fig. 5 Portion of the radula ribbon and teeth of the baicaliid species (**A–Ad**) *Baicalia turiformis* (**B–Bd**) *Teratobaicalia ciliata* (**C–Cd**) *Maackia herderiana* (**D–Dd**) *Maackia costata*. Scale bars: **A–D** = 0.1 mm; **Aa–Dd** = 10 μ m



but this study indicates that their differences are also likely to have a strong functional component. Our demonstration that radula size can vary among species independently of shell size suggests a selective importance for this character. Similarly, the statistically significant differences in fine scale morphological characters of radular teeth, such as tooth and cusp size and number of cusps, suggest that our focal snail species have distinctive patterns of food particle collection. Jorgensen (2001) showed that significant differences in cusp and tooth morphology

among three *Lacuna* species (Littorinidae) were closely related to dietary differences.

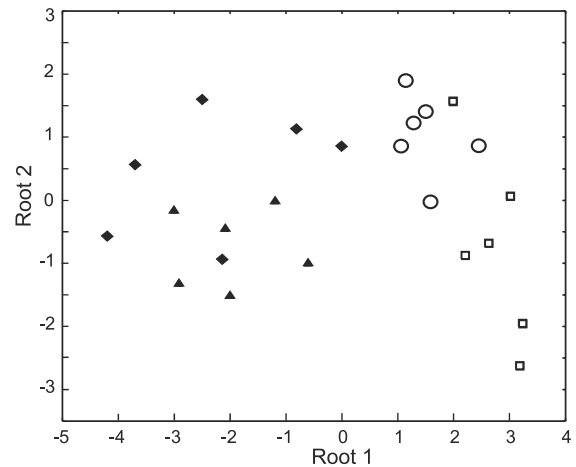
Ctenidial filter feeding has been described for marine and freshwater gastropods in more than ten families and is common in suspension feeders with a microphagous herbivorous diet (Deckerck, 1995). Young snails of some species use ctenidial filter feeding whereas adults are mostly grazers, thus trophic ontogeny shows a directed shift between the two feeding modes (Tashiro & Colman, 1982; Brendelberger & Guergens, 1993; Navarro

A Wilk's lambda = 0.001, approx. $F(48,78) = 12.976$, $p < 0.0000$ **Fig. 6** Discriminant analyses of baicaliid radular tooth measurements. **A** Plot of the first three roots of 18 variables in size of the teeth and cusps (see Table 4, characters 1, 2, 4, 5, 7, 8,

& Chaparro, 2002). Some ctenidial filter feeding gastropods consume suspended or deposited matter in relation to accumulate of total nitrogen and organic carbon in their surrounding sediments (Kamimura & Tsuchiya, 2004). Trophic ontogeny has yet to be demonstrated in baicaliids, but it seems a likely possibility for species that are able to burrow in soft sediment. The suggestion that the ctenidium of baicaliids is linked to food acquisition patterns is supported by our results. Food particles enter the mantle cavity with the water flow, which is likely to be influenced the number of gill leaflets. The particles then become covered by mucus and form a cord which is captured by the radula (Röpstorf et al., 2003).

Valvatids have an external ctenidium that cannot be used for filter feeding. Observing the feeding behavior of *M. baicalensis* under the light stereo microscope, we found that they do indeed filter, but with a mechanism that relies on cilia which cover the lips of the mouth. Valvatids have long rostrum, which they move close to surface of the substrate. It is possible that valvatids are rather “interface filter feeders” (Dauer et al. 1981) and are able to utilize suspended matter hanging on vertical stone and sponge substrates.

In conclusion, we have used multiple lines of evidence to demonstrate that five sympatric gastropod species on rocky walls of underwater canyons of

B Wilk's lambda = 0.061, approx. $F(12,45) = 7.087$, $p < 0.0000$ **B** Plot of the first two roots for 4 cusp variables (see Table 4 characters 3, 6, 9, 12)

Baikal assimilate different components of the benthos and seston. This model system indicates that fine scale differences in radulae can result in differences in resource use, with reducing competition and permitting diverse assemblages with high population densities.

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