On morphological and ecological evidence of adaptive differentiation among stony cliff littoral Baikal gastropods

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ABSTRACT
Three morpho- or ecotypes (‘ribbed’, ‘middle’ or ‘ribless’ shell and ‘smooth’) of lithophilous *Maackia herderiana* (Lindholm, 1909) (Caenogastropoda: Baicaliidae) were investigated along the hydrodynamic zones of four locations on the southwestern littoral of Lake Baikal in southeast Siberia. We found a prevalence of the ribbed-shell morphotype inhabiting stones at a depth of 1.2–2.0 m, corresponding to the hydrodynamic zone of strong wave activity, and a predominance of the smooth-shell morphotype living on cliffy canyons at 21–31 m depth in the hydrodynamic zone where wave action is very weak or totally absent. Mixed groups of snails with ribbed, ribless and/or smooth shells were present on stony-boulder substrates at 3 to 15–19 m depth of the wave-cut and wave-weakening hydrodynamic zones. Ribbed-morphotype snails living in inshore and wave-cut hydrodynamic zones had a smaller shell size than did smooth-morphotype snails inhabiting zones where wave activity was weak or totally absent. The thickness of ribbed shells in the non-ribbed areas was equal to the thickness of smooth shells; ribs enhance the thickness of the shell by 3–4 times, thereby increasing the strength of ribbed shells against destructive wave action. On the basis of the different correlation coefficients of shell weight, soft body mass and total mass with increasing shell height, we assumed a growth differentiation between the ribbed and smooth morphotypes. We compared our results with data on ecotypes of some freshwater and marine gastropods.

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Introduction
Lake Baikal in southeast Siberia, like other ancient lakes of the world, is a natural laboratory for the study of endemic lacustrine speciation. There are 117 known species of endemic Baikal gastropods in Lake Baikal, 40 of which belong to the Baicaliidae family (Sitnikova et al. 2004), and many questions about their origins remain obscure. One of these questions relates to the adaptive differentiation along habitat gradients among lithophilous littoral species. Most of the baicaliids (24 species) occupy soft sediments at different depth zones down to 240 m of the lake. In littoral zones down to 20 m depth there are eight species that live on mixed sediments and eight only found on solid substrates (pebbles, stones, boulders, rocks and cliffs) (Sitnikova et al. 2004).
The shallow water zone of ancient lakes of the world, including Lake Baikal, is extremely heterogeneous and enriched with a variety of habitats, and it is here that benthic invertebrates display extraordinary species diversity (Michel 1994; Wilke et al. 2009; Vadeboncoeur et al. 2011). Thus, these shallow habitats should be considered a zone where parapatric speciation predominates (Schreiber et al. 2012).

According to Karabanov (1990), the formation of Baikal littoral environments depends on the underwater landscape, which is primarily determined by the wave impact on the mobility of bottom sediments. On the basis of hydrodynamic characteristics, he divided the Baikal littoral into three zones: (A) the inshore zone (0–2 m depth) of destructive wave activity and undertow flows; (B) the wave-cut zone (2–5 m); and (C) the wave-weakening zone (5–20 m). Strong wave action dislocates hard substrates up to 30 cm in size and tears off algae in the inshore hydrodynamic zone. In the wave-cut zone, wave strength is about 2–4 times less than in the inshore zone, and waves are able to remove substrates up to 5 cm in size. In the wave-weakening zone, the wave strength is up to 25 times less than the other two zones, and at times of high wave action the maximum size of moving sediments is about 5 mm at 11 m depth and 2 mm at 20–30 m depth (Karabanov 1990; Potemkina et al. 2005).

These vertical zones extend along the entire shoreline of Lake Baikal, but the boundaries of each one change due to local particularities (Karabanov 1990). Similarly, the four bottom underwater complexes (beach, shallow-water terrace, underwater slope and underwater canyon) in Baikal littoral landscapes were defined by Kravtsova et al. (2004). The authors showed the mosaic spatial distribution of biological communities along these complexes, and the dominance of gastropods in most of the communities. Baicaliids (2–11 coexistent species) prevailed among littoral gastropod assemblies, and small snails of *Maackia herderiana* (Lindholm 1909) were the dominant species among the baicaliids, inhabiting all three hydrodynamic zones and the four bottom underwater complexes on solid sediments (Kravtsova et al. 2004; Sitnikova et al. 2010; Maximova et al. 2012). The snails of *M. herderiana* have been subdivided (Kozhov 1936) into three morphologically distinct forms or subspecies denoted as ‘ribbed’ (*M. h. herderiana*), ‘middle’ or weakly defined ribs (probably *M. h. semicostulata* Lindholm, 1909) and ‘smooth’ (*M. h. laevis* Kozhov, 1936) (Figure 1). All of these forms may be found in the geographical locality of the stony cliff littoral of southern Lake Baikal. The reasons for the intraspecific differentiation of this species compared with freshwater and marine gastropods have not yet been investigated, and a conjecture for the possible initial step of parapatric speciation of Baikal gastropods along hydrodynamic depth zones in solid littoral has not yet been proposed.

In this study, we examined lithophilous *M. herderiana* morphs inhabiting neighbouring sites on the southwestern littoral of Lake Baikal to (1) determine the proportion of the three morphotypes in each hydrodynamic zone, and (2) observe the differences in morphological traits of each morphotype, including shell thickness and weight, to understand whether these differences are associated with their habitats.

Materials and methods

Sites and samples

Snails of *M. herderiana* (Caenogastropoda: Baicaliidae) were randomly collected by SCUBA divers at four locations along the southwestern shore of Lake Baikal.
Figure 1. Shell images of smooth (A–C), ribless (D) and ribbed (E–G) morphotypes of *Maackia herderiana* with the measurements used in the morphological study. (C, G), top view and measuring the number of whorls. H = shell height; W = shell width; aw = aperture width; al = aperture length; ah = aperture height; hz = spire height; ho = height of last whorl; ht = height of two subsequent whorls; h1 = height of the first whorl over the aperture; w1 = width of the first whorl over the aperture; l1 = length of the first whorl over the aperture; a1 = convex of the first whorl over the aperture; characteristics h2–h3, w2–w3, l2–l3, a2–a3 were measured as the first whorl over the aperture. Scale bars: 1 mm.
Information about the regions, locations, dates of the sampling, habitats and treatment of the samples is given in Table 1. Samples were collected from three hydrodynamic zones: (A) the inshore zone down to 2 m depth; (B) the wave-cut zone at 3–4 m depth; and (C) the wave weakening-zone, divided into the Cbs zone (the beginning of the slope at 8 m), the Cs zone (the slope down to 18 m depth) and the Cc–zone (the canyons at 15–31 m). The distances of the different depth zones from the shore at the sampling sites are not constant (Table 1); they fluctuate with season in all Baikal littoral zones and depend on the angle of the bottom inclination (Karabanov 1990).

A total of 2102 individuals of *M. herderiana* were divided into three morphotypes: ‘ribbed’ shell with tall and stout ribs visible on all whorls (Figure 1E–G); completely ‘smooth’ shell without any ribs (Figure 1A–C) and ‘ribless’ morph with weakly defined, short and thin ribs visible on 1–3 whorls (Figure 1D). Only 217 shells were used in the morphometric analysis. The shells were photographed and 20 linear shell variables were measured using the Image-Pro Plus software package (Figure 1A). The number of whorls of each shell was also calculated (Figure 1C).

Shell thickness was measured across the transverse breaking at the last whorl (Figure 2) from scanning electron microscope (Quanta 200) images. To determine the ratio between the shell mass and soft body mass of each morph, only individuals with intact shells were used. Individuals were weighed on an electronic balance to the nearest 0.01 mg, and then their soft bodies were isolated and weighed separately. The shell mass (weight) was calculated as total mass minus soft body mass. The material was slightly dried with filter paper before weighing.

To minimise the contribution of ontogenic variability in the shell variables to the analyses, young snails <4–5 years in age were not used, as shell growth is significantly slower in adults of this species (Maximova et al. 2007).

### Table 1. Geographical regions, collection dates, characteristics of the sampling sites and number of the individuals for treatment. 1 = ratio of morphotypes; 2 = shell morphometry; 3 = shell thickness and weight.

| Location                      | Date          | Depth (m) | Distance from shore (m) | Characteristics of sampling sites | Treatment of samples |
|-------------------------------|---------------|-----------|-------------------------|----------------------------------|----------------------|
| Listvenichny Bay              | September 2011| 1.5–2     | 6–10                    | Inshore (A)                       | 77, 80, 203          |
| 51°51′ N 104°50′ E           |               | 3–4       | 70                      | Wave-cut (B)                      | 5                    |
|                               |               | 15        | 150                     | Weakening of wave (Cc)            |                      |
|                               |               |           |                         | Stones                            |                      |
| Berezovy Cape                 | August 2003   | 1.2–1.5   | 50                      | Inshore (A)                       | 93, 342, 389         |
| 51°50′ N 104°53′ E           |               | 3–4       | 290                     | Wave-cut (B)                      | 28, 30                  |
|                               |               | 8         | 730                     | Weakening of wave (Cbs)           | 20, 39                |
|                               |               |           |                         | Stones                            |                      |
|                               |               |           |                         | Stony top of the slope            | 186, 326              |
|                               |               |           |                         | Stones on the slope               | 150                   |
|                               |               |           |                         |                                 |                      |
| Bolshie Koty Bay, Varanchka   | February 2013 | 2–3      | 60–80                   | Wave-cut (B)                      | 163                  |
| 51°54′ N 105°05′ E           |               |           |                         | Boulders                          |                      |
| Bolshie Koty Bay, Zhilische   | August 2005   | 3.2–4    | 80–100                  | Wave-cut (B)                      | 100, 269              |
| 51°53′ N 105°03′ E           |               | 9         | 110–120                 | Weakening of wave (Cc)            | 31, 30                |
|                               |               |           |                         | Boulders                          |                      |
|                               |               |           |                         | Cliff, canyon                     | 200, 48              |
|                               |               |           |                         |                                 |                      |
Statistical analyses

The differences among morphotype proportions found for each hydrodynamic zone were tested using Pearson’s χ² test. Data on shell morphology were tested for normal distribution using a Kolmogorov–Smirnov test. We used canonical discriminant analysis (CDA) using the 20 derived linear shell variables to evaluate differences in shell characteristics among the three morphotypes. Shell variables were analysed using analysis of variance (ANOVA) with morphotype and wave impact as independent factors, followed by Tukey’s honestly significant difference post hoc test. Statistical analyses were conducted using the STATISTICA-8 software package.

Results

Ratio of morphotypes

The ratios of the three morphotypes of adult *M. herderiana* differed among the three hydrodynamic zones (Figure 3). Ribbed-morphotype snails prevailed in the inshore zone (A); they accounted for 96–97% of *M. herderiana* in Listvenichny Bay and near Berezovy Cape. The number of ribbed snails in zone A of both sites was significantly higher (Pearson’s χ², p < 0.00) than in the wave-cut zone (B), where the proportions of ribbed shells were still high –66 and 75%, respectively. On the canyon at a depth of 15 m (Listvenichny Bay) and on the slope at a depth 18 m (Berezovy Cape), both belonging to the wave-weakening zone (C), the smooth morphotype made up 87 and 65%, respectively. The percentage of ribless individuals was 12% in Listvenichny Bay and 24% in Berezovy Cape. It should be noted that mostly ribbed shells (99%) were registered at the

![Figure 2. Transverse breaking at the last shell whorl of ribbed (A–C) and smooth (D–E) morphotypes. TR1 = maximum rib convexity of a ribbed shell; TR2 = thickness of non-ribbed place of a shell; TS = thickness of a smooth shell. Scale bar: 300 μm.](image)
beginning of the slope in the wave-weakening hydrodynamic zone (Cbs) in Berezovy Cape (Figures 3 and 4).

In zone B of Bolshie Koty Bay, the proportion of ribbed shells was 14% in Varnachka and 21% in Zhilische (Figure 3). The dominance of smooth-morphotype snails in Varnachka (48%) and ribless snails in Zhilische (50%) resulted in a different intraspecific
composition of *M. herderiana* between the Bolshie Koty and Berezovy–Listvenichny localities (*p* < 0.00).

Smooth shells prevailed among snails found on the clifffy canyon at 19–31 m depth of zone Cc in Zhilische, which was similar to what was observed for the wave-weakening zone (Cc and Cs) in Listvenichny Bay and Berezovy Cape (Figure 3).

The number of smooth shells found in the wave-weakening zone (C) was significantly higher (*p* < 0.00) than in the other hydrodynamic zones over all localities.

Despite the variability in the occurrence of the morphotypes at the sampling sites, we found a prevalence of ribbed shells at 1.2–2.0 m depth (hydrodynamic zone A, where wave activity is strong) and a predominance of the smooth morph at 21–31 m depth (hydrodynamic zone Cc, where wave action is very weak or totally absent). Mixed groups of snails with strong ribbed, slightly ribbed and/or smooth shells were present at depths from 3 to 15–19 m of the wave-cut and wave-weakening zones in different proportions at the localities.

### Shell morphometry

 Canonical discriminant analysis of 20 shell characteristics revealed the significant difference (Wilks’ *λ* = 0.09; χ² = 236.99, df = 36, *p* < 0.00) between the ribbed and smooth morphotypes inhabiting the inshore (A) and the slope down to 18 m depth (Cs) hydrodynamic zones, respectively, near Berezovy Cape. The clouds of these two morphs do not overlap on the plane of Root I and Root II of the CDA (Figure 5), but both considerably overlap with the snails of the neighbouring hydrodynamic zone and depth – that is, the ribbed morphotype of zone A at 1.2 m depth overlaps with the ribbed morph of zone B at 3 m depth, which overlaps with the cloud of the ribbed morph from zone Cbs at 8 m depth. The last cluster overlaps with the smooth morphotype at 18 m depth in zone Cs. The first canonical discriminant function explained 88.8% of the morphometric variance (canonical correlation = 0.92) and the second canonical discriminant function explained 11.2% (canonical correlation = 0.62).

![Figure 5](image-url). Canonical roots provided by discriminant analysis run for three morphotypes. A = inshore zone; B = wave-cut zone; Cbs = wave-weakening zone from the beginning of the slope; Cs = wave-weakening zone on the slope; Cc = wave-weakening zone on the canyons.
Similarly, the ribless (3–4 m depth in zone B) and smooth morphs (21–31 m depth in zone Cc) from Zhilische were represented by non-overlapping clouds on the plane of Root I and Root II of the CDA (Figure 5). Both clouds overlapped with the cloud of smooth shells from zone Cs at 19 m depth, also from Zhilische. The discriminant index successfully distinguished between the ‘ribless’ and ‘smooth’ morphotypes (Wilks’ $\lambda = 0.08; \chi^2 = 257.57, df = 28, P < 0.00$). The first canonical discriminant function explained 85.4% of the morphometric variance (canonical correlation = 0.92) and the second canonical discriminant function explained 14.6% (canonical correlation = 0.70).

The morphometric analyses showed that the size of the smooth shells from zone C were significantly larger than those of ribbed and ribless individuals from zones A and B in both the Berezovy (ANOVA, $F = 5.73, p = 0.00$) and Zhilische ($F = 11.82, p = 0.00$) localities (Figure 6).

At Berezovy Cape, the individuals of the ribbed morphotype from zone A were significantly different from the ribbed individuals from zone B in eight shell characteristics (Figure 6, characteristics 2, 4, 8–10, 13, 14, 17). The ribbed and smooth morphotypes living at 8 and 18 m depths, respectively, in zone C differed in 12 shell variables (Figure 6, characteristics 1, 2, 4–11, 16, 17).

There was a significant difference in 15 shell characteristics (Figure 6, characteristics 2–5, 8–18) between shells collected from zone B in the Berezovy and Zhilische localities. The shell size of the smooth morphotype from zone Cs (at 18 m depth) at Berezovy Cape was significantly larger than the shell of the same morphotype living in zone Cs (at 19 m depth) at Zhilische (Figure 6, characteristics 1, 2, 4–10, 12–14, 16–18), and did not differ from specimens of zone Cc (at 21–31 m depth) at Zhilische (Figure 6, characteristics 2, 4–17).

Thus, ribbed-morphotype snails living in inshore and wave-cut hydrodynamic zones were smaller than smooth-shelled snails inhabiting zones where wave activity was weak or totally absent.

**Shell thickness and weight**

Measurements of shell thickness and weight revealed significant differences between the ribbed and smooth morphotypes. In areas of maximum rib convexity (Figure 3), ribbed shells were 3–4 times (Tukey’s honestly significant difference test, $p < 0.00$) thicker than smooth shells (Figure 7, TR1 and TS), whereas in non-ribbed areas of shell, the morphs did not differ in thickness at all ($p = 0.85$; Figure 7, TS and TR2). We consider that the ribs increase the strength of shells against destructive wave action.

With increasing shell height, we observed a reliable increase in the total mass (Figure 8A) and soft tissue mass (Figure 8C) for both morphs, with different correlation

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**Figure 6.** Shell measurements of the morphotypes from different locations. Mean values marked by the same letter are not significantly different [one-way analysis of variance (ANOVA), Tukey’s honestly significant difference test, $p \geq 0.05$]. Eighteen of the 21 characteristics are plotted; the three other characteristics were similar among the three morphotypes and are not shown here. A = inshore zone; B = wave-cut zone; Cbs = wave-weakening zone from the beginning of the slope; Cs = wave-weakening zone on the slope; Cc = wave-weakening zone on the canyons.
coefficients. The shell mass (Figure 8B) did not increase with shell growth of smooth individuals, and became smaller in the ribbed morph. Among snails with equal values of total mass (Tukey’s honestly significant difference test, \( p = 0.38 \)), the shell weight of the smooth morphotype was on average 10% less than that of the ribbed \( (p < 0.00) \), and reached 66% of the total snail weight, whereas the shell weight of the ribbed morph was up to 75% of the total mass. The soft tissues of the smooth morphotype weighed more than those of the ribbed \( (p < 0.00) \). These distinctions possibly indicate the growth differentiation between the ribbed and smooth morphotypes.

Discussion

Shell morphotypes and habitats

There are as many similarities (phenotypic variation) as differences in the sculpture characteristics among marine and some freshwater gastropods, including the Baikal snail *M. herderiana*, the shell of which is cross-ribbed in the zone of strong wave action and smooth in the calm zone. For example, the existence of two (or sometimes more) morphs (or ecotypes) is well known, especially among marine gastropods of *Littorina* (Littorinidae) and *Nucella* (Muricidae), which inhabit different localities along environmental gradients with different degrees of wave exposure of rocky sediments (Boulding et al. 1999; Rolán et al. 2004; Guerra-Varela et al. 2009; Johannesson et al. 2010), and among the freshwater genera *Leptoxus*, *Pleurocera*, *Semisulcospira* and *Lithasia*.
Figure 8. Correlation of mass variables with shell height of the ribbed and smooth morphotypes.
(Pleuroceridae) living in fluvial or stream conditions (Urabe 2000; Minton et al. 2008; Dillon 2011; Whelan et al. 2012). There are data on morphological differentiation of *Radix auricularia* (L., 1758) depending on wave-exposed habitats in open Baikal littoral or conventional habitats for this palaearctic snail (Stift et al. 2004). Spyra and Strzelec (2013) showed a highly significant association of two subspecies of pulmonate *Armiger crista* (L., 1753) differing in shell sculpture with leaf deposits and *Typha* remains, while associations with different physicochemical properties of water were not revealed. Two ecotypes of marine *Nucella lapillus* living on different sites of Galician Atlantic shores (Spain) differ in some phenotypic characteristics; the shells of the exposed morph that lives outside estuaries are devoid of spiral cords, whereas the sheltered ecotype typically living inside estuaries has spiral cords on the shell (Rolán et al. 2004). Several studies on the phenotypic differentiation of *Littorina saxatilis* in rocky and boulder habitats show that morphs differ according to wave action on the Swedish west coast (Janson 1983; Janson and Sundberg 1983; Johannesson et al. 1993), the northwest coast of Spain (Cruz et al. 1998; Carballo et al. 2005) and the northern coast of England (Grahame et al. 2006). Similar eco-morphological differentiations are also known in *Littorina sitkana* (Boulding et al. 1999), *L. scutulata* (Hohenhohe 2003) and *L. striata* (Wolf et al. 1998). Gastropod surveys have also revealed vertical differentiation into ecotypes along horizontal geographic regions. For example, two (H and M) ecotypes of *L. saxatilis* are widespread across four sites in the northwestern region of the British Isles, about 50 km apart (Wilding et al. 2002). Grahame et al. (2006) investigated the adaptation to a steep environmental gradient of both ecotypes (H and M) of *L. saxatilis* distributed on rock walls around and above boulder fields, and the boulders themselves, on two UK shores (Thornwick Bay and Old Peak). They concluded that microhabitat differentiation could favour different shell shapes.

In this study, phenotypic differentiation of the focal species *M. herderiana* was observed along an environmental gradient in southwestern Baikal littoral, where ribbed and smooth morphotypes dominated on different hard substrates, i.e. stone-boulder fields and cliff walls, situated in different hydrodynamic zones. We considered here the distribution of three morphotypes of the lithophilous Baikal endemic species along three dependent abiotic factors (depth, wave activity and type of substrate), although there are many other abiotic and biotic factors maintaining the heterogeneity of environments in the Baikal littoral (e.g. Kravtsova et al. 2004). As the boundaries of the hydrodynamic zones are different in different regions of the Baikal littoral, the size of the bottom substrates is not equal and a wave force at the same depth of different geographical regions is dissimilar; thus, this is one of the reasons for the distinct compositions of morphotypes among the sampling sites.

Johannesson (2003) noted that populations of nine *Littorina* species having planktrophic larvae are not subdivided into phenotypes living in wave-exposed and wave-sheltered sites. All 10 species of *Littorina* with direct larval development are characterised by strong phenotypic variation among populations inhabiting different types of habitats. Note the focal species *M. herderiana*, like all Baikal gastropods, is a direct developer using hard substrates for the attachment of egg masses.
Shell size and habitats

Other than differentiation in shell sculpture, there are differences in shell size amongst gastropods and bivalves adapted to different hydrodynamic environments. Amongst freshwater clams of the family Sphaeriidae, those inhabiting rapid rivers with unstable substrates and powerful floods have the heaviest and most robust shells (Alimov 1981). The massive shells (84–89% of the total mass of the organism) of marine bivalves of the genus Astarte represent an adaptation to gravel–pebble substrata, aiding in this clam’s survival there despite the mechanical effect of the shifting, unstable substratum (Prena et al. 1999; Zettler 2002; Hermsen et al. 2003; Selin 2007). Experiments have shown that ribbed shells of the freshwater snail Semisulcospira reiniana are more tolerant of crushing load than smooth shells with the same shell mass (Urabe 2000).

The sheltered ecotype of marine Nucella lapillus shows ridges, an apparently relatively smaller aperture and thicker shell than the smooth, exposed ecotype (Rolán et al. 2004; Guerra-Varela et al. 2009). According to Palmer (1981), skeletal growth can limit the rate of body growth: both thick- and thin-shelled morphs of Nucella lamellosa produce shell material at a remarkably similar rate during maximum growth, but thick-shelled snails exhibit a significantly slower rate of body growth. The relative shell-lip thickness of dogwhelks was greater in residents at a wave-exposed site than in those at a sheltered site: juveniles from a sheltered site were transferred to a wave-exposed site and after 1 year they had developed a thicker shell-lip (Pascoal et al. 2012). The shells of the exposed ecotype of L. saxatilis are thinner and smaller with a larger aperture than the sheltered ecotype (Johannesson et al. 1993; Boulding et al. 1999; Rolán-Alvarez 2007).

In M. herderiana, we observed some peculiar properties – the ribbed morphotype with relatively small and thick shells occurred at sites with strong wave action, while the smooth morphotype with thin and prolonged large shells occupied localities where wave action was absent. Before stating that ecotypes are confined to specific habitats and completely associated with adaptation of snails to such environments, it is necessary, in our opinion, to discuss possible effect of predation.

Ribbed shell and predation

Predators have strong effects as selective agents on morphological shell variation in gastropods (Boulding et al. 1999; Johannesson 2003; Carballo et al. 2005; Grahame et al. 2006; Preston and Roberts 2007; Glaubrecht and von Rintelen 2008; Minton et al. 2008; Narvarte et al. 2008). For example, the sheltered ecotype of L. saxatilis represents a specific adaptation to an extreme microhabitat and resists predation risks (Rolán-Alvarez 2007). Some experiments (Sepulveda et al. 2012) have shown that thin, sheltered snails of Acantina monodon (Muricidae) are able to change their shell morphology as a direct response to predators (crabs); besides a morphological response, the snails produce a thickening of the shell, which can occur without direct contact between the snails and crabs. There is a striking diversity of adaptations among gastropods in Lake Tanganyika, East Africa, that signals the evolution of unique intra- and inter-generic morphologies and behaviours as strategies for predator defence (West and Cohen 1996). It has been shown that for two species of the genera Lavigeria from Lake Tanganyika, the more sculptured snail L. coronata is less frequently killed by crab Platytethysa armata and
more frequently damaged than the other species *L. grandis* (Rosales et al. 2002). As a rule, freshwater, shell-breaking molluscivores (such as crabs, crayfish, prawns and fishes) prefer thinner-shelled prey (Covich 2010).

Gastropods account for only ~6% of the food particles of grayling and three species of sculpins (*Cottoidei*) dwelling in the littoral of Berezovy Cape (one of the sampling sites); these fish mainly consume benthic amphipods (Maximova 2007; Tolmacheva 2008) as well as most of the Baikal endemic *Cottoidei* fishes (Sideleva and Mekhanikova 1990). Gastropods prevailed (84% of gut contents) in the diet of the cyprinid *Rutilus rutilus* during summer fattening in the inshore and wave-cut zones at Berezovy Cape (Maximova 2007). Two gastropod species with smooth shells, *Megalovalvata baicalensis* (Gerstfeldt) (Valvatidae) and *Maackia bithyniopsis* (Lindholm) (Baicaliidae), were the most abundant components (75 and 20%, respectively) in gut contents of roach, whereas snails of the ribbed morphotype of *M. herderiana* were recorded in a small quantity (< 1%) of 7% of fish guts (Maximova 2007).

Attacks on Baikal shallow-water snails by predator flatworms and amphipods are not known. We assume that the more robust shell of the ribbed morph of *M. herderiana* makes it tolerant to predation; however, at present, we cannot prove this. In any case, the ribbed morphotype of *M. herderiana* with thicker, heavy, small-sized shells is associated with an increased risk of shell-breaking.

**Remarks on partial reproductive isolation and speciation**

The distribution of ecotypes of *M. herderiana* has some analogy with the marine snail *Littorina saxatilis* (Janson and Sundberg 1983; Johannesson 2003). Despite a clear difference in shell morphology between the two ecotypes of *Littorina saxatilis*, the intermediate population overlaps both. This population is present in high numbers in an intermediate zone that varies from 5 to 20 m in width (Janson and Sundberg 1983; Johannesson 2003). In another example, a stable hybrid zone is produced across a vertical shore gradient a few metres in length (Rolán-Alvarez 2007). Although each ecotype still shows a preference for a particular microhabitat (Kostylev et al. 1997; Carballo et al. 2005), the two ecotypes meet and occasionally mate in overlapping environments, where they produce apparently fertile, intermediate morphological forms (Rolán-Alvarez et al. 1999). In our case, the co-occurrence of ribbed, smooth and middle *M. herderiana* ecotypes suggests the existence of a hybrid zone that extends to different distances in relation to the distance of local hydrodynamic zones.

Males of *Lavigeria coronata* in Lake Tanganyika moved significantly farther than females; the average net travel distance was 50 cm d⁻¹, equal to 20 times the shell length (Michel et al. 2007). The two ecotypes of *Littorina saxatilis* are able to move within the range of 1–4 m per 3 months, and migration distances since time of release are on average greater in the sheltered than in the exposed habitats (Janson 1983). One of the two sub-populations of *Littorina brevicula*, a common species in the upper intertidal zone of Amakusa (Japan), migrates to the lower zone in the winter, while the second stays in the upper zone (Takada 1995). Migrations of female and male *M. herderiana* in a natural environment are unknown. We observed cultivated snails, which cover a distance of 10 cm (10–15.5 times as long as the shell height) in 1 hour. We assume that
wave impact in the summer and autumn prevents the active migration of the snails and interbreeding between ecotypes from different hydrodynamic zones. Passive migration of snails with a water mass during storms remains unknown. During the ice period, the wave ecological barrier between ecotypes disappears and the ecotypes have the opportunity to move simultaneously between the hydrodynamic zones, and between neighbouring southern and northern regions.

The origin and development of reproductive isolation among ecotypes of *Littorina* has been extensively debated (Johannesson 2003; Grahame et al. 2006; Rolán-Alvarez 2007; Bultin et al. 2008; Sadedin et al. 2009; Johannesson et al. 2010; Butlin et al. 2014). These authors supposed that the ecotypes of *Littorina* originated independently in different parts of Europe (in England, Spain and Sweden), but that there was a single origin within each region. Johannesson et al. (2010) proposed that several different non-allopatric mechanisms can explain the repeated evolution of the *L. saxatilis* ecotypes.

Possibly, the ecotypes of the focal species *M. herderiana* from Lake Baikal should be considered in this context too. Webster et al. (2012) discussed the role of habitat choice in reproductive isolation and ecological speciation and described three independent criteria underlying 10 different evolutionary scenarios in which habitat choice may promote or maintain local adaptation. We hope that the next few years will witness a methodological and conceptual revolution in the study of Baikal endemic gastropods to resolve the problem of intraspecific differentiation and speciation along short-distance environmental gradients.

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