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Lymnaeid snails in the city of Salzburg – A malacological and ecological study in the urban area

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Abstract: In the present contribution, stagnant and running waters situated in the city of Salzburg were investigated for their colonization by the pond snails *Radix labiata* and *R. balthica*. Besides a comprehensive cartographic determination of gastropod distribution across the urban area, also new aspects with regard to the ecological behaviour of the molluscs could be obtained. Malacological and ecological study of 60 sample points located in all parts of the city yielded evidence that *R. labiata* is characterized by slightly wider distribution (occurrence at 68% of all sample sites) than *R. balthica* (occurrence at 62% of all sample sites). For both species, high abundances (>10 individuals per m^2) were measured in ponds enriched with submerged vegetation, whereas spring-fed brooks with coarse mineral substrate were either completely devoid of the animals or contained only very small populations (<1 individual per m^2). According to ecological modeling based on Weighted Average Analysis and the computation of marginality and tolerance, *R. balthica* bears higher potential to occupy ecological niches than *R. labiata*.

Key words: Pond snail, faunistic mapping, urban water system, ecological modelling, aquatic biotope, ecological niche.

Introduction

In the past century, mapping of the freshwater malacofauna evolved into a main activity field of biologists in Central Europe. Besides a comprehensive malacological documentation of rural areas interspersed with various types of stagnant and running waters, also numerous urban territories were subjected to a rigorous survey with regard to their colonization by aquatic gastropods and bivalves (see reviews in: FALKNER 1990, PATZNER 1995, GLÖER 2002, GLÖER & MEIER-BROOK 2003). In Germany, among other the cities of Altenberg (BAADE 1989), Frankfurt an der Oder (BOETTGER 1926), Braunschweig (GRABOW 1994), Hamburg (GLÖER 2002), and Darmstadt (GROH 1984) were included in respective malacological mapping campaigns. In Austria, the cities of Salzburg (see review in PATZNER 1995) and Vienna (FRANK et al. 1990) were investigated for their colonization with aquatic molluscs. Thereby, it could be verified that both the biodiversity and specific abundance of the malacofauna exhibit a negative correlation with the extent of control structures realized in urban rivers and lakes (OSBORNE et al. 1993, STATZNER & SPERLING 1993, STURM 2010). In other words, straightening measures of running waters or all kinds of embankments commonly result in a dramatic reduction of the macrozoobenthic fauna including most gastropods and bivalves, because formerly natural habitats undergo abrupt changes with regard to their environmental conditions. Most species and above all those acting as specialists do not have the ability to adapt to rapid modifications of their environment, whereas generalists dispose of a better chance of surviving the habitat modifications largely unharmed (STURM 2003, 2004, 2010, 2012, 2013).

If a closer look is taken on the malacological documentation of the city of Salzburg, a mapping history covering a time-span of almost 80 years can be recognized (PATZNER 1995, STURM 2000a, 2010).Whilst in earlier times main focus of the biological field work was placed on larger running waters (Salzach, Glan) and ponds in the southern urban areas (e.g., MAHLER 1949, HANUS 1997), more recent mapping campaigns increasingly considered smaller water bodies in the northern and eastern part of the city (e.g., PATZNER & ISARCH 1999, STURM 2000a, 2010). After summing up the results outlined in all these studies, it may be concluded in correspondence with the remarks noted above that small waters devoid of valuable anthropogenic impact bear highest biodiversities and specific abundances. In contrast, waters exhibiting enhanced degrees of control structures or higher levels of pollution are remarkably depauperate concerning their aquatic fauna. Among freshwater molluscs, this process of species pauperization, however, chiefly involves animals with lower ecological tolerance (e.g., Bithyniidae, Valvatidae, Planorbidae), whereas organisms with enhanced adaptability (e.g., Lymnaeidae, Sphaeriidae) partly undergo significant reproduction.

Two gastropod species tolerating increased environmental burdens and thus acting as generalists in many aquatic biotopes are *Radix labiata* and *R. balthica* (GLÖER & MEIER-BROOK 2003, STURM 2000a, 2000b, 2000c, 2003, 2004, 2006, 2007, 2012, 2013). Although the distribution of these two pond snails in the city of Salzburg has been already explored to some degree, there are still numerous open questions with regard to the individual ecology and colonization behaviour. In order to partly overcome this deficit, the present contribution pursues two main goals: The first objective consists in the presentation of current distribution data for the two gastropod species in the city of Salzburg. The second objective comprises the ecological characterization of *Radix labiata* and *Radix balthica* by combining these distribution data with related measurements of physical and chemical water parameters. Here, Weighted Average Analysis (WAA), a powerful mathematical technique for the solution of ecological problems, finds its application.

Material and Methods

Ecology of the studied gastropod species

As outlined in numerous ecological studies (e.g., FALKNER 1990, TURNER et al. 1998, GLÖER 2002, GLÖER & MEIER-BROOK 2003, STURM 2001, 2007, 2012, 2013), both *Radix labiata* and *R. balthica* are largely ratable as generalists, which has conferred the ability on them to rank among those pioneer species colonizing the Alpine regions. In general, the alpine pond snail *Radix labiata* is frequently found in small stagnant and running waters with a high stock of plants. Occasionally, it can be also collected from puddles and marshy pools, which are characterized by temporary drying up (STURM 2000). Due to its pulmonary respiration the gastropod species is capable to overcome small distances on arid ground, thereby migrating from one aquatic habitat to another

(STURM 2012, 2013). The oviform pond snail *R. balthica* disposes of an ecological profile being very similar to that of *R. labiata*. In addition to small water bodies the gastropod also colonizes larger rivers as well as aquatic biotopes with slightly brackish water chemistry (up to 14‰ salt content; GLÖER & MEIER-BROOK 2003). The snail commonly feeds on green algae, diatoms, and detritus and is further marked by Palaearctic distribution, according to which it can be also observed in Iceland (GLÖER 2002). All pond snails are distinguished by their hermaphroditism, which gives them the ability to switch between sexual and asexual reproduction and to induce rapid increase of the population.

Date and performance of gastropod sampling

Investigation of various waters located in the city of Salzburg for their stock of the two pond snail species was carried out from May to September 2016. Within this time period, physical and chemical characteristics of the studied brooks and ponds exhibited a certain constancy, with respective measured data varying between 0.2 and 5%. Altogether, 25 water bodies including 17 brooks and 8 ponds were sampled for gastropods. Among the locations investigated for this contribution, about 40% are situated in the northern half of the city, whereas the remaining 60% belong to the southern half (Fig. 1).

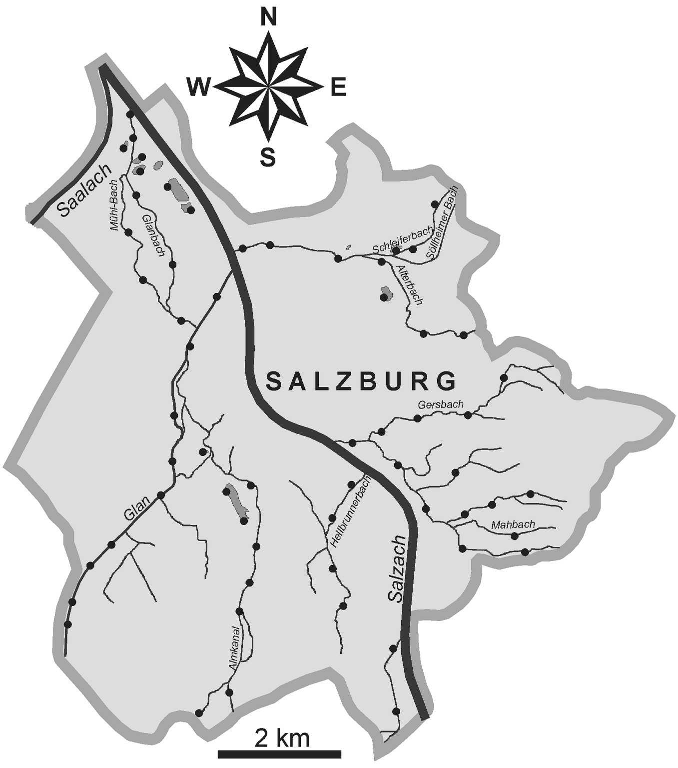


Fig. 1: Geographic map of the city of Salzburg with all sample locations investigated for the possible colonization by pond snails.

Those brooks rising in the east mostly run through undulating landscape with variable vegetative cover. All running waters flow in the Salzach representing the main river of Salzburg that crosses the city in north-south direction.

Sampling strategy included the collection of snails by sieving the ground sediment and examining larger stones as well as plants for their stocking with respective animals (STURM 2007, 2012). For statistical purposes, a total area of about 10 m² was subjected to malacological analysis at each sample point. Collected individuals belonging to each species were quantified numerically and subsequently released to their habitats again. Only for documentation, single representatives sampled at the locations were fixed in alcohol and stored in the author's archive.

Elicitation of physico-chemical parameters and data processing

At each sample point environmental conditions of the colonized habitats were approximately determined by measurement of biological, physical and chemical water parameters. Physical quantities included water temperature (°C), mean grain size of the ground substrate (cm), current velocity (m s^{-1}) in the case of brooks, water depth (cm), shading of the water body by riparian vegetation (%), whereas quantification of submerged vegetation including algal cover of stones (%) was evaluated as biological parameter. Chemical quantities, on the other hand, comprised of the pH-value, aquatic concentration of oxygen (mg L^{-1}), nitrate content in the water (mg L^{-1}), total water hardness (°dH), and biological oxygen demand after five days (BOD_5; mg L^{-1}). Most parameters were analyzed by using simple tools such as measuring tape, thermometer, and portable measuring instruments (STURM 2007, 2012). For accurate quantification of the BOD_5-value, water was sampled, measured for its O_2-content and afterwards filled into a hermetically sealable flask. After storage of the vessel in a dark room for five days, the content of oxygen was quantified again, and the difference between the two measured concentrations was classified as BOD_5-value.

In order to work out ecological specificities of *Radix labiata* and *R. balthica*, site-specific measured values obtained for single environmental parameters were combined with related quantitative animal data and submitted to a Weighted Average Analysis (WAA). Application of this mathematical method includes the computation of species-weighted mean values and standard deviations for each biological, physical and chemical factor (STURM 2012, 2016). These statistical parameters can be subsequently used for the determination of specific preferences with regard to given environmental conditions. For an appropriate differentiation between generalistic and specialistic behaviour, the Global Marginality Coefficient (GMC) and Global Tolerance Coefficient (GTC) recently outlined by STURM (2012, 2013, 2016) were modeled for each environmental parameter. As demonstrated by the author, low values of the GMC commonly indicate a preference of the studied organism for 'standard' conditions, whereas high values of the GMC attest a certain potential of the animal for the occupation of ecological niches. Low values of the GTC may be interpreted as result of restricted organismic tolerance with regard to a given environmental parameter, whilst high values of the GTC may be discussed as a consequence of enhanced tolerance.

Results

Evaluation of environmental parameters

Main statistical results of environmental parameter analysis are summarized in Tab. 1. Concerning water temperature measured at 60 sample locations, a mean value of 13.8±3.2°C was computed (range: 12.4°C) indicating a rather broad spectrum of thermal conditions among the studied waters. A rather contrary behaviour was found for the pH-value assuming a mean of 7.0±0.3 (range: 1.3) and thus representing a rather balanced concentration of hydrogen ions in the water bodies. For electric conductivity a mean value of 238.5±33.6 µS cm^{-1} (range: 140.4 µS cm^{-1}) was evaluated. This measured quantity is indicative of an increased content of Ca^{2+} and Mg^{2+} ions in the aquatic habitats. Oxygen content in the water amounts to 10.0±1.0 mg L^{-1} (range: 4.2 mg L^{-1}), and the related oxygen saturation may be quantified with 95.9±5.6% (range: 21.1%). This circumstance speaks for a sufficient supply of most waters with oxygen. Nitrogen concentration in the water assumes a mean value of 2.6±0.7 mg L^{-1} (range: 2.5 mg L^{-1}), which indicates rather low anthropogenic load of the brooks and ponds included in this study. This is also underlined in part by the BOD_5 amounting to 2.1±0.5 mg L^{-1} (range: 1.9 mg L^{-1}). Water hardness has to be evaluated as rather high (mean: 17.5±2.5°dH, range: 10.3°dH) and provides a hint for the predominance of limestone building the geological base of the city. Mean water depth, at which the gastropods were sampled, was measured with 137.8±31.6 cm (range: 123.5 cm), whereas current velocity amounted to 0.5±0.3 m s^{-1} (range: 1.2 m s^{-1}). For grain size of the mineral sediment a mean of 1.9±0.4 cm (range: 1.5 cm) could be found. Shading of the sample sites assumed a mean of 49.6±20.9% (range: 91.5%), whilst submerged vegetation including algal cover of stones and plants was measured with 52.5±22.8% (range: 84.4%).

Tab. 1: Results of the statistical evaluation of single environmental parameters and output of WAA. Asterisks mark significant differences ($P < 0.05$) of weighted averages between *Radix labiata* and *Radix balthica*. Abbreviations: CV...current velocity, D...water depth, EC...electric conductivity, GS...grain size, N_2...nitrogen content in water, O_2...oxygen content, O_2s...oxygen saturation, S...shading, SV...submerged vegetation, T...water temperature, WH...water hardness.

	T	PH	EC	O_2	O_2s	N_2	BOD_5	WH	D	CV	GS	S	SV
MEAN	13.8	7.0	238.5	10.0	95.9	2.6	2.1	17.5	137.8	0.5	1.9	49.6	52.5
SD	3.2	0.3	33.6	1.0	5.6	0.7	0.5	2.5	31.6	0.3	0.4	20.8	22.8
RANGE	12.4	1.3	140.4	4.2	21.1	2.5	1.9	10.3	123.5	1.2	1.5	91.5	84.4
R. labiata													
WA	14.4	7.0	235.6	9.7	94.3	2.3	2.2	17.3	143.7	0.4	1.8	49.3	51.3
WSD	1.5	0.6	19.6	0.8	8.1	0.2	0.2	1.4	14.6	0.1	0.1	5.5	6.9
R. balthica													
WA	*13.3	7.0	236.6	10.0	94.4	2.2	2.0	17.4	*133.5	*0.3	*2.0	49.5	*57.7
WSD	1.7	0.9	29.2	1.3	11.9	0.3	0.3	2.1	17.0	0.1	0.3	7.1	9.2

Occurrence of the two pond snail species

Animal collection procedure conducted at the single sample points came to the result that 41 locations out of 60 (68%) are characterized by the presence of *Radix labiata*, whereas 38 locations (62%) are colonized to a highly variable extent by *R. balthica*. The urban distribution of the two gastropod species is summarized in the maps of Fig. 2. Thereby, it is conspicuous that mainly the northern and southern parts of the city of Salzburg including higher numbers of stagnant water bodies represent regions of enhanced specific abundance. In the eastern and western parts, where a predominance of variably sized running waters is given (Fig. 1), the pond snails are principally marked by restricted occurrence.

Highest abundance of *Radix labiata* could be attested for the largest pond of the city ("Leopoldskroner Weiher"), where partly more than 10 individuals per m^2 could be collected at the selected sample site. In the other stagnant waters dispersed across the city, abundances commonly ranged from 1 to 10 gastropods per m^2. A partly contrary situation became apparent for the running waters, where specific abundance could be routinely extrapolated to less than 1 individual per m^2. In the case of *R. balthica*, colonization behaviour bore a great likeness to that of *R. labiata*. In ponds with remarkable density of submerged vegetation, the gastropod partly occurred with higher frequency than its closely related species. Whilst in the "Leopoldskroner Weiher" an abundance of more than 10 individuals per m^2 could be extrapolated, in most brooks with stony substrate and reduced vegetative stocking abundance of the species declined to less than 1 individual per m^2 or could not be measured anymore due to the complete absence of the animals.

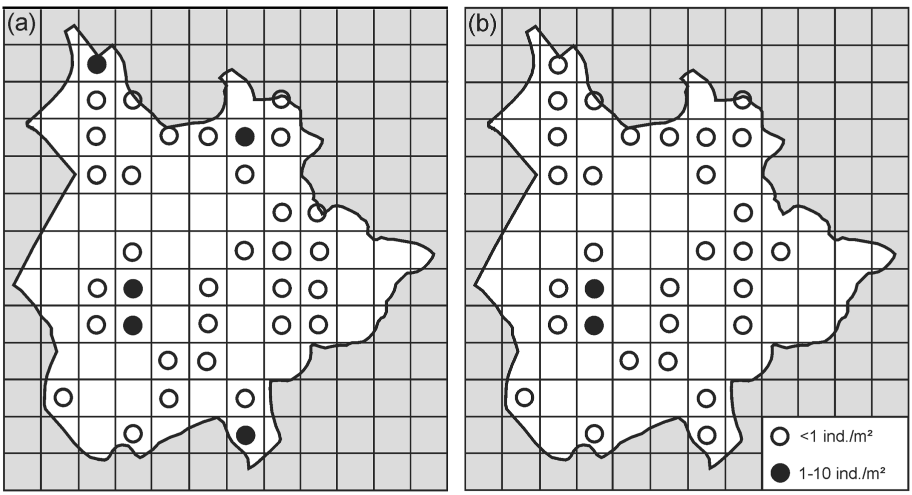
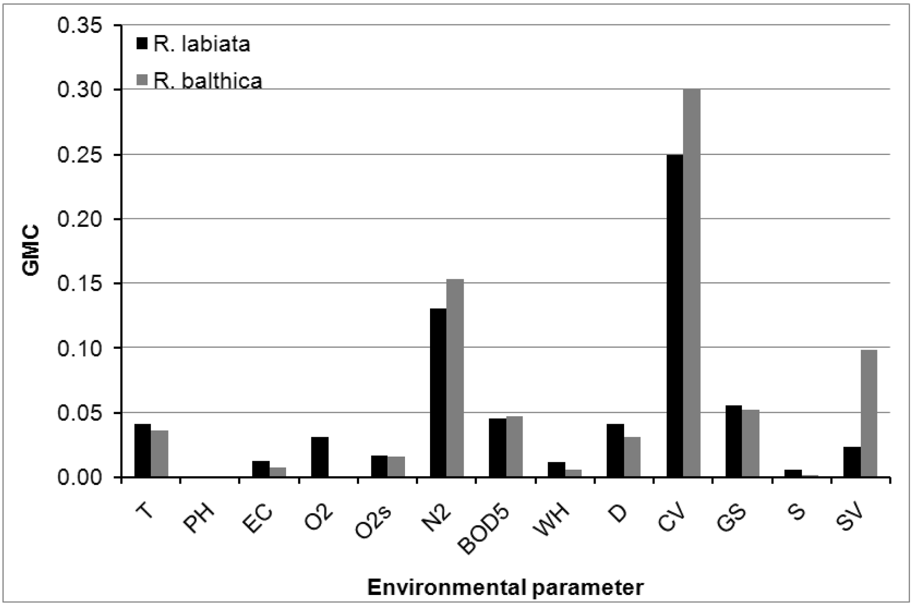


Fig. 2: Urban distribution maps computed for *Radix labiata* (**a**) and *R. balthica* (**b**). The first gastropod species could be collected at 68% of all sample locations, whereas the second one was restricted to 62% of the studied sites.

(a)



(b)

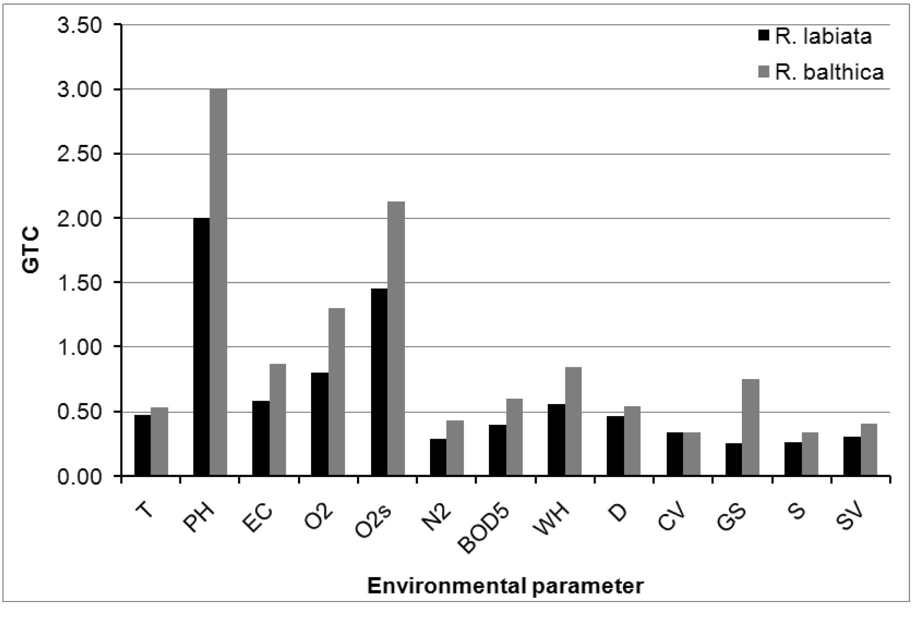


Fig. 3: Global Marginality Coefficient (GMC; a) and Global Tolerance Coefficient (GTC; b) modeled for the different environmental parameters (Abbreviations: see Table 1).

Results of WAA and ecological characterization of the pond snails

Computed results for weighted average (WA) and weighted standard deviation (WSD) are summarized in Tab. 1. Concerning water temperature, respective statistical parameters assume values of 14.4±1.5°C (*Radix labiata*) and 13.3±1.7°C (*Radix balthica*). According to the output data obtained from parametric testing of the mean values (Student's T-test), difference between the two weighted averages has to be construed as significant with $P < 0.05$. With regard to the pH-value, both gastropod species are characterized by nearly identical statistical parameters. This circumstance is also largely verified for electric conductivity, oxygen content in the water, oxygen saturation, aquatic nitrogen concentration, BOD_5, and water hardness, although weighted standard deviations partly exhibit valuable differences between the species due to varying tolerances towards some environmental parameters (see below). In the case of water depth, the weighted parameters determined for *Radix labiata* amount to 143.7±14.6 cm and differ significantly ($P < 0.05$) from those computed for *Radix balthica* (133.5±17.0 cm). A similar situation is given for current velocity (0.4±0.1 m s^{-1} versus 0.5±0.1 m s^{-1}) and grain size of the mineral sediment (1.8±0.1 cm versus 2.0±0.3 cm). In terms of shading, both gastropod species exhibit identical statistical behaviour, whereas respective weighted averages measured for the stock of the aquatic biotopes with submerged vegetation are again marked by significant discrepancies ($P < 0.05$).

Specific Global Marginality Coefficients computed for all environmental parameters are depicted in Fig. 3a. Thereby, it is conspicuous at first glance that they commonly range from 0 to 0.30 and are sometimes remarkably lower for *Radix labiata* than for *R. balthica*. In other words, *Radix labiata* is partly characterized by lower ecological marginality than *R. balthica*. Except for aquatic nitrogen concentration and current velocity, GMC values of both species remain below a threshold of 0.1 and thus may be regarded as indicative for pronounced generalistic behaviour. In the case of current velocity, the respective GMC value computed for *Radix labiata* levels out at 0.25, whereas that determined for *Radix balthica* consistently exceeds 0.30.

Global Tolerance Coefficients calculated for the two pond snails and all environmental parameters are depicted in Fig. 3b. In general, respective values range from 0.25 to 3.00 and are continuously higher for *Radix balthica* than for *R. labiata*. According to the ecological computations highest tolerance is expressed toward the pH-value, followed by oxygen content in the water (oxygen saturation), electric conductivity, and water hardness. For most of the remaining environmental parameters, GTC values of both species fall below 1 and therefore indicate a rather restricted tolerance.

Discussion and Conclusions

As demonstrated in several previous studies (e.g., BAADE 1989, HANUS 1997, GLÖER 2002, STURM 2009), urban water bodies commonly differ from rural ones in several aspects: In the case of running waters, partly extensive river bank stabilization has significantly contributed to minimize all damage caused by floods. Besides these building activities, urban rivers and lakes situated near larger settlement areas also undergo an increased exertion of anthropogenic influence, which is reflected by massive encroachment on the natural biotopes and deterioration of water quality. According to ecological investigations on the macrozoobenthos colonizing urban waters (PATZNER 1995, STURM

2000, 2009, 2013, GLÖER & MEIER-BROOK 2003), man-made modifications of aquatic habitats are not easily tolerated by numerous species and, most of all, not by those being adapted to very specific environmental conditions. Such specialists are found in typical urban waters only in very exceptional cases.

In the city of Salzburg, largely untouched running and stagnant waters of the North and South are confronted with obstructed rivers and brooks of the West and East, which mainly served as water suppliers for industry and mill races in the past (HANUS 1997, PATZNER & ISARCH 1999, STURM 2009). Whilst natural waters bear a rather high faunal biodiversity, rectified and fully artificial waters are significantly depauperate with regard to insects, molluscs, arthropods and other animals. The rivers and ponds investigated for this contribution largely confirmed this impression. In the present study, ecological investigations were purposely limited to the pond snails *Radix labiata* and *R. balthica*, because these two gastropod species are acknowledged in the scientific literature as generalists with the potential to colonize partly extreme habitats (TURNER et al. 1998, GLÖER & MEIER-BROOK 2003, STURM 2007, 2012, 2013). Although both gastropods could be collected at a majority of sample locations (*R. labiata* at 68% and *R. balthica* at 62% of all sample sites), they preferably occurred in all those waters characterized by marginal anthropogenic influence (Fig. 2).

Detailed ecological analyses conducted with the help of WAA yielded evidence that both pond snails are distinguished by their largely poikilothermic behaviour and thus colonize both colder and warmer water bodies. This predicate allows them to spread in waters of the Alpine foreland (STURM 2000, GLÖER & MEIER-BROOK 2003), but also in lakes of increased Alpine height levels (TURNER et al. 1998, STURM 2007, 2012). Here, the ecological behaviour of the gastropods stands in a clear contrast with that of other species being specialized in narrower temperature intervals (e.g., *Bythinella austriaca*; STURM 2005, 2016). With regard to the pH-value, *Radix labiata* and *R. balthica* mainly prefer neutral conditions, but can be also found in slightly acidic and alkaline waters (STURM 2013). Both gastropod species exhibit a rather indifferent behaviour towards electric conductivity of the water and can be collected from aquatic habitats enriched with or depleted of oxygen. The non-sensitiveness to the concentration of O_2 in the water is largely attributable to the circumstance that pond snails belong to the pulmonate gastropods, which get a certain amount of air supply in their shells (FALKNER 1990, GLÖER & MEIER-BROOK 2003).

With regard to the concentration of nitrogen in the water, which may be evaluated as typical indicator of anthropogenic influence, the pond snails behave rather intolerant and are thus adaptable to fluctuating chemical conditions only to a certain degree (Fig. 3). This limited adaptability has to be regarded as result of the live custom exhibited by the gastropods: both species may be found in rather small aquatic habitats with high density of submerged vegetation and lower aeration of the water, where metabolic processes inevitably lead to rapid modifications of dissolved nitrate and nitrogen (GLÖER & MEIER-BROOK 2003, STURM 2013). Contrary to the nitrogen content in the water the BOD_5 and total hardness have only a minor effect on the distribution of the pond snails in the urban waters. Here, it has to be restricted, however, that BOD_5 values measured at the sample points largely point towards good water quality and marginal pollution with bacterial organisms. Reactions of the gastropods to extreme conditions of microbiotic activity (reflected by high BOD_5 values) are still underexplored due to the lack of appropriate data collected in the field or obtained from laboratory experiments. In this case, an intensification of scientific efforts is highly desirable in future.

Concerning physical parameters describing the aquatic habitats, *Radix labiata* and *R. balthica* are partly distinguished by lower tolerances to any fluctuations. Both species prefer shallow waters, where they either colonize the bottom substrate or occupy the stalks and leaves of water plants (PATZNER 1995, STURM 2000, GLÖER 2002). A clear ecological diagnosis is provided with regard to the current velocity, because according to the results of this study the pond snails tend to populate slowly running or stagnant waters, whereas spring-fed brooks with rapid flow either exhibit strongly reduced population densities or are completely avoided by the gastropods (STURM 2007, 2013). Grain size of the bottom substrate and shading of the water bodies have only minor effects on the urban distribution of *R. labiata* and *R. balthica*, which predestines both species to colonize brooks and ponds in very exposed locations (TURNER et al. 1998, STURM 2007, 2012). Similar to current velocity also the stock of aquatic biotopes with submerged vegetation may be regarded as limiting factor of colonization insofar as both pond snails show a preference for higher vegetative density, because they mainly feed on detritus and algae covering the plants and stones (GLÖER & MEIER-BROOK 2003).

Based upon the computation of the GMC and GTC, ecological characteristics of *Radix labiata* and *R. balthica* are partly marked by significant discrepancies (Fig. 3). In general, *R. balthica* tends to develop higher marginality than *R. labiata* and therefore bears a slightly higher potential to populate ecological niches. This phenomenon is expressed very evidently with regard to aquatic nitrogen concentration, current velocity, and density of submerged vegetation. Additionally, *R. balthica* is consistently characterized by higher tolerance towards environmental parameters than *R. labiata*, which also underlines a certain pioneering nature of this gastropod species (TURNER et al. 1998, GLÖER & MEIER-BROOK 2003).

From the results presented in this contribution it is concluded that both pond snails have to be largely evaluated as generalists and thus may represent essential elements of the urban macrozoobenthos. As demonstrated for the running and stagnant waters situated in the city of Salzburg, *Radix labiata* and *R. balthica* show rather high tolerances towards most physical, biological, and chemical factors influencing their environment, which brings them a certain adaptability to any anthropogenic impacts. Ecological modeling yielded a certain evidence for the increased ability of *R. balthica* to occupy ecological niches. Here, it has to be stated restrictively that computation of ecological factors was solely based upon data obtained from urban water analyses and faunistic cartography in the city of Salzburg. Therefore, statements respecting animal-environment interactions can be only generalized to a certain degree and further ecological studies will be necessary in future.

Zusammenfassung

Lymnaeidae in der Stadt Salzburg − Eine malakologische und ökolgische Studie im urbanen Raum

Im vorliegenden Beitrag wurden stehende und fließende Gewässer der Stadt Salzburg auf ihre Besiedlung durch die Schlammschnecken *Radix labiata* und *R. balthica* untersucht. Neben einer ausführlichen kartografischen Bestimmung der Schneckenverbreitung im urbanen Raum gelang es auch, neue Aspekte hinsichtlich des ökologischen Verhaltens der Weichtiere zu gewinnen. Die

malakologische Untersuchung von insgesamt 60 über das ganze Stadtareal verteilten Probenpunkten ergab, dass *R. labiata* eine etwas weitere Verbreitung (Auftreten bei 68 % aller Probenpunkte) besitzt als *R. balthica* (Auftreten bei 62 % aller Probenpunkte). Für beiden Arten konnten hohe Abundanzen (> 10 Individuen/m²) vor allem in jenen mit submerser Vegetation angereicherten Stillgewässern ermittelt werden, wohingegen Quellbäche mit grobem mineralischen Substrat entweder frei von jeglichem Besatz mit Schlammschnecken waren oder lediglich über sehr begrenzte Populationen (< 1 Individuum/m²) verfügten. Gemäß ökologischer, auf dem Prinzip der gewichteten Mittelwertsanalyse basierender Modellrechnungen, welche die Kalkulation entsprechender Marginalitäts- und Toleranzfaktoren miteinschlossen, besitzt *R. balthica* ein geringfügig höheres Potenzial zur Besetzung ökologischer Nischen als *R. labiata*.

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