Hydrobiologia (2016) 765:71–83
DOI 10.1007/s10750-015-2402-2

PRIMARY RESEARCH PAPER

Does narrow niche space in a 'cold-stenothermic' spring snail indicate high vulnerability to environmental change?

Michael Klockmann · Mareike Scharre · Martin Haase · Klaus Fischer

Received: 31 March 2015 / Revised: 30 June 2015 / Accepted: 3 July 2015 / Published online: 15 July 2015

Abstract Niche breadth has fundamental ecological implications. Specialists with a narrow niche space are able to survive under specific conditions only, making them potentially sensitive to effects of environmental change. We here investigate (1) the factors restricting the specialized spring snail *Bythinella dunkeri* to its specific habitat, and (2) its capacity for plasticity to respond to changing environmental conditions, based on a combination of field work and laboratory experiments. By comparing occupied and unoccupied sites, we revealed that snail presence was most strongly affected by distance to the crop-out, water depth, pH value, and redox potential. In contrast, spring temperatures did not affect the occurrence of this 'stenothermic' snail, and laboratory experiments documented a high tolerance toward both high and fluctuating temperatures. However, *B. dunkeri* was found to be very sensitive to desiccation, such that changes in precipitation regimes may easily harm populations. The species investigated here may therefore indeed be sensitive to environmental change, but not because of limited thermal tolerance which initially seemed to be the most obvious reason.

Handling editor: Verónica Jacinta Lopes Ferreira

M. Klockmann (✉) · M. Scharre · M. Haase · K. Fischer
Zoological Institute and Museum, University of Greifswald, Johann-Sebastian-Bach-Str. 11/12, 17489 Greifswald, Germany
e-mail: klockmannm@uni-greifswald.de; Michael.klockmann@uni-greifswald.de

Keywords *Bythinella dunkeri* · Springs · Habitat preference · Climate change · Desiccation resistance · Thermal tolerance

Introduction

Niche breadth, which is defined as the range of environments or resources that a species is able to inhabit or use (Gaston et al., 1997), is an ecological concept being of fundamental importance. This is because niche breadth may be the crucial factor underlying the commonness and rarity of species, and may therefore also affect their extinction risk (Slatyer et al., 2013). Arguably, species that are able to use a broader range of resources and/or to maintain viable populations under a wider variety of environmental conditions should be more common and widespread, which is expected to result in a positive correlation between niche breadth and geographical range size (Brown, 1984; Slatyer et al., 2013). The according niche breadth-range size hypothesis has been addressed in numerous studies, and a recent meta-analysis suggests that it is a general ecological pattern (Slatyer et al., 2013).

Given such wide-ranging implications of niche breadth it seems, at first glance, counter-intuitive that some species are highly specialized and thus restricted to specific habitats (narrow niche space), while other species with more generalist life styles thrive under a variety of environmental conditions (broad niche space; Thuiller et al., 2005; Ricklefs, 2010). Several reasons have been suggested to promote specialization despite obvious drawbacks, including, for instance, a more efficient resource use and escaping from competition or predation (Fox & Morrow, 1981). The concomitant adaptation to specific environmental conditions may in turn preclude survival under alternative conditions (Swihart et al., 2002). Consequently, specialists are deemed particularly sensitive to environmental change such as human-induced climate change (Johnson, 1998; Thuiller et al., 2005). Therefore, it is important to understand (1) the factors restricting specialized species to specific habitats, and (2) their capacity for plasticity to respond to changing environmental conditions. The second issue may be of special importance as genetic adaptation, as opposed to phenotypic plasticity, may not be fast enough to keep track with ongoing changes (Parmesan & Yohe, 2003; Bradshaw & Holzapfel, 2006).

Against this background, we here investigate the habitat preferences and capacity for plasiticity in the highly specialized spring snail *Bythinella dunkeri* (Frauenfeld, 1857). Spring-dwelling species seem to be particularly suitable to examine the consequences of a narrow niche space for various reasons. Springs are unique and, in general, rare and isolated ecosystems that are located at the interface of ground and surface water (Benke et al., 2009). These ecosystems are characterized by relatively constant physical and chemical conditions (Cantonati et al., 2006), which change rapidly with increasing distance from the crop-out (McCabe, 1998). Springs often provide suitable habitat for rare including relict species (Lindegaard et al., 1998; Di Sabatino et al., 2003), and many species are completely restricted to springs (Illies, 1978). Such ‘crenobionts’ are typically highly specialised to their constant environment, being not able to colonize habitats other than springs (Hoffsten & Malmqvist, 2000). In this context temperature may be of utmost importance, as most of these species are believed to be cold-stenothermic (Jungbluth, 1973). Consequently, the specialised species communities of springs could be particularly sensitive to changing conditions, which may be caused by habitat loss and degradation or climate change, posing major threats to extant biodiversity (Sala et al., 2000; Thomas et al., 2004). Dispersing to other habitats is often difficult due the high degree of habitat isolation (Cushman, 2006), although passive transport may be an option for some such organisms (Boag, 1986; Dillon, 2000; Delicado et al., 2014). Here, transport by water birds is one possibility (Figuerola & Green, 2002), but data proofing this are lacking for *Bythinella* so far (Falniowski & Szarowska, 2011).

Bythinella dunkeri is a Central European water snail being confined to springs and spring-fed brooks (Oswald et al., 1991), which probably has a low evolutionary potential (Brändle et al., 2005) like other *Bythinella* species (Falniowski & Szarowska, 2011). Our study is based on a two-step approach. First, we investigated the habitat preferences of *B. dunkeri* in the Westerwald mountain range (Germany) by comparing occupied and unoccupied springs as well as occupied and unoccupied locations within springs. Thus, our first goal is to find out the factors limiting *B. dunkeri* occurrence. Comparisons are mainly based on hydrological and chemical parameters, which typically determine the distribution of freshwater snails (Ponder & Colgan, 2002). We did not include biotic factors as it was expected the species to be limited in the first place by abiotic factors (Sturm, 2005).

Second, we assessed capacity for plasticity in the tolerance toward thermal, desiccation, and pH stress under laboratory conditions, factors which are predicted to limit the distribution of the species (Sturm, 2005). Our second goal thus is to explore to which extent the species is able to cope with changing environmental conditions. Specifically, we predict that (1) snails prefer permanently cold, unpolluted springs with a neutral pH, and that (2), due to its high specialization to such habitats, its capacities to tolerate increasing temperatures, low pH values, and desiccation are very low, exemplifying the high sensitivity of such species to environmental change and providing a mechanistic link for the species’ restriction to spring habitats.

Materials and methods

Study organism

The genus *Bythinella* (Bythinellidae, not Hydrobiidae; see Wilke et al., 2013) consists of a relatively large number of species which are very similar in terms of ecology and morphology, though taxa occurring in different geographical regions are genetically distinct

(Benke et al., 2009, 2011; Falniowski & Szarowska, 2011). The genus is nowadays mainly restricted to mountainous regions throughout central and southern Europe including the Balkans and Asia Minor, but was probably more widespread in the Pleistocene (Benke et al., 2009). *Bythinella dunkeri* is one of these small water snails ($\leq$3 mm), being confined to unpolluted springs and adjacent spring-fed brooks (Oswald et al., 1991). Its range is basically restricted to mountain ranges in western and south-western Germany and some bordering areas (Oswald et al., 1991). The species may have reached central Europe from southern refugia after the last glacial period, which may indicate a relatively high dispersal ability and perhaps even a broader niche space than expected (Benke et al., 2009). *B. dunkeri* mainly feeds on cyanobacteria, diatoms, and algae, and population density can be up to 9500 individuals per m^2 in appropriate habitats (Oswald et al., 1991). Eggs are deposited as 'capsules' which are attached to stones, leaves, or aquatic plants (Oswald et al., 1991). Development to adulthood takes ca. 17 weeks at 8°C, and the maximum lifespan is >2 years (Oswald et al., 1991). The species is threatened by spring destruction, eutrophication, pollution, acidification, and by drying-up of springs (Reiss, 2011). It is considered to be a vulnerable species in Germany (Jungbluth & Knorre, 2009).

Study area and field survey

In order to study habitat preferences, we investigated 30 springs in the Westerwald mountain range (Rhineland-Palatinate, western Germany), located within the center of the species' distribution range. The selected springs are small though probably discharging all year round. The study area is characterized by a mountainous climate with an annual mean temperature of 7.5°C and a precipitation of 1163 mm per year (Wetterdienst, 2014). The Westerwald belongs geologically to the Rhenish Slate Mountains, with the main bedrock being basalt (Steingötter, 2005). For each spring, we recorded the number of *B. dunkeri* individuals at 4-6 sampling points ($N = 132$ in total) between October 7th and 13th 2013. The first sampling point was always located right within the crop-out of the spring, and the others at 50–100 m intervals downstream the spring-fed brooks (maximum distance to crop-out: 450 m). Each sampling point was carefully searched for *B. dunkeri* individuals for exactly 10 min, paying special attention to structures on which the species can be typically found (e.g., stones, leaves).

Per sampling point we recorded 17 environmental parameters, also between October 7th and 13th 2013. These included parameters describing the surroundings of the springs as well as several physical and water-chemical characters (Table 1a, b). Distance to crop-out, surroundings, shadowing, structure, substrate type, and substrate diversity (i.e., number of different substrate types, $n = 1$–4) were assessed in the field by visual inspection. The different surroundings occurring around sampling points were transformed to numbers [grassland (1), beech forest (2), alder forest (3), spruce forest (4), mixed forest (5)]. Shadowing was estimated as the percentage of ground covered by trees and bushes. The structure of the spring/brook was only subjectively classified and also transformed into numbers. It was considered natural (3) if there were no obvious signs of anthropogenic habitat degradation, semi-natural (2) when there were small signs of anthropogenic habitat degradation (e.g., course changes) and artificial (1) in cases of strong human impact such as straightening or spring tapping. The different substrate types occurring per sampling point were transformed into numbers as follows: sand (1), sand+stones (2), mud (3), sand+mud (4), sand+stones+mud (5), solid ground (6); other combinations did not occur. Solid ground refers to genuine rocks. Stream current (surface velocity) was determined using the drift body method by measuring the time a small foam ball (diameter 1 cm) needed to cover a distance of two meters. Spring/brook depth and width were recorded thrice with a folding rule in the immediate vicinity of the sampling points. The mean of the three measurements was used for further analyses. Temperature, pH, conductivity, redox potential, oxygen concentration, salt concentration, acid binding capacity, and phosphate concentration were measured directly in the spring water with a multifunctional measuring device (PCE pHD1; PCE Instruments Germany). Finally, acid-binding capacity and phosphate concentration were analyzed colorimetrically (Aqua Merck) by taking water samples, which were always analyzed the same day.

Eight out of the 30 springs were additionally equipped with a total of 41 data loggers (iButton DS1923), which recorded water temperature once per hour between June 3rd and October 7th 2013. The loggers were placed within small plastic cups filled

Table 1 Comparison of environmental parameters (means ± 1 SE) between occupied ($N = 63$) versus unoccupied ($N = 69$) sampling points (a) and between the sampling points located in occupied ($N = 80$) versus unoccupied ($N = 52$) springs (b)

Parameter	Occupied	Unoccupied	*Z*	*P*
(a)				
Distance to crop-out (m)	84.76 ± 12.61	148.55 ± 12.05	−3.11	**0.0019**
Surroundings	3.06 ± 0.09	2.68 ± 0.09	0.96	0.3353
Shadowing (%)	75.40 ± 2.73	69.86 ± 2.61	1.22	0.2230
Structure	2.06 ± 0.09	1.68 ± 0.09	2.56	**0.0105***
Substrate type	3.41 ± 0.21	3.01 ± 0.20	1.52	0.1275
Substrate diversity	1.81 ± 0.09	1.67 ± 0.08	0.98	0.3285
Stream current (m/s)	0.08 ± 0.01	0.07 ± 0.01	0.83	0.4070
Depth (cm)	2.31 ± 0.29	4.30 ± 0.28	−5.75	**<0.0001**
Width (cm)	59.84 ± 5.07	60.04 ± 4.84	−0.54	0.5862
Temperature (°C)	9.56 ± 0.18	9.29 ± 0.17	1.08	0.2823
pH	7.13 ± 0.08	6.64 ± 0.08	3.58	**<0.0001**
Conductivity (μS/cm)	141.00 ± 6.94	143.32 ± 6.64	−0.71	0.4773
Redox potential (mV)	212.22 ± 8.37	185.61 ± 8.00	2.19	**0.0286***
Oxygen concentration (mg/l)	38.49 ± 1.55	38.98 ± 1.48	−0.33	0.7429
Salt concentration (%)	0.01 ± <0.01	0.01 ± <0.01	−0.06	0.9528
Acid binding (mmol/l)	1.23 ± 0.07	0.98 ± 0.07	3.75	**0.0002**
Phosphate concentration (mg/l)	0.17 ± 0.05	0.29 ± 0.05	−1.22	0.2238
(b)				
Distance to crop-out (m)	117.00 ± 11.75	119.81 ± 14.57	−0.21	0.8315
Surroundings	3.15 ± 0.17	2.69 ± 0.21	1.87	0.0615
Shadowing (%)	74.50 ± 2.42	69.42 ± 3.01	0.60	0.5480
Structure	2.06 ± 0.08	1.56 ± 0.10	3.27	**0.0011**
Substrate type	3.40 ± 0.19	2.90 ± 0.23	1.64	0.1016
Substrate diversity	1.78 ± 0.08	1.65 ± 0.10	0.99	0.3235
Stream current (m/s)	0.09 ± 0.01	0.06 ± 0.01	2.25	**0.0109***
Depth (cm)	2.31 ± 0.29	4.30 ± 0.28	−5.02	**<0.0001**
Width (cm)	63.80 ± 4.47	54.02 ± 5.54	0.40	0.6888
Temperature (°C)	9.61 ± 0.16	9.13 ± 0.19	1.78	0.0749
pH	7.13 ± 0.07	6.47 ± 0.08	4.98	**<0.0001**
Conductivity (μS/cm)	141.27 ± 6.16	143.66 ± 7.64	1.15	0.2510
Redox potential (mV)	208.66 ± 7.44	182.39 ± 9.23	2.25	**0.0242***
Oxygen concentration (mg/l)	40.11 ± 1.36	36.65 ± 1.69	1.55	0.1221
Salt concentration (%)	0.01 ± <0.01	0.01 ± <0.01	0.16	0.8705
Acid binding (mmol/l)	1.22 ± 0.06	0.91 ± 0.08	4.95	**<0.0001**
Phosphate concentration (mg/l)	0.17 ± 0.04	0.33 ± 0.05	−1.74	0.0820

Differences were tested for significance using Mann–Whitney *U* tests. Significant *P* values are given in bold. * Not significant anymore after sequential Bonferroni correction

with sand and were fixated using stones and cord. They were positioned within the center of the respective sampling points, i.e., the first logger was located right within the crop-out of the spring and the others further downstream. All springs equipped with loggers were known to be inhabited by *B. dunkeri* to investigate the effects of temperature variation on snail density.

Experiments on capacity for plasiticity

We performed three experiments to explore the plastic responses of *B. dunkeri* to (1) temperature, (2) desiccation, and (3) pH. All snails for these experiments were collected from the above springs in the Westerwald mountain range. Snails for experiments

(1) and (2) stemmed from seven and for experiment (3) from three different springs. The collected animals were transferred to Greifswald University, where they were kept in standardised water, i.e., a mixture of tap and de-ionized water (1:5) showing similar chemical properties (in pH, conductivity) as compared with the springs from which snails were collected. Then, snails were transferred to a climate cabinet (Sanyo MLR-351 H) set at 8°C for 5 (experiments 1 and 2) or 14 (experiment 3) days for acclimation. For experiments, the snails from each spring were randomly distributed among treatments. Throughout, snails were fed ad libitum by providing beech leaf litter inoculated with microorganisms. For experiments (1) and (3), they were transferred to plastic boxes (250 ml) filled with the above-standardized water, using 10 individuals per box. For experiment 2 see below.

Experiment 1: thermal tolerance

After the acclimation period, snails were randomly distributed among seven thermal treatments: (1) permanent temperature of 8°C (reflecting current conditions, control); (2) permanent temperature of 12°C, mimicking a temperature increase by 4°C through global warming; (3) 12 h at 8°C and 12 h at 12°C per day, mimicking the diurnal temperature cycle in spring-fed brooks; (4) 5 days at 8°C and 5 days at 18°C per 10 days, mimicking the impact of a heat wave; (5) 12 h at 12°C and 12 h at 24°C per day to test whether snails will survive more extreme conditions, which they will probably never encounter in nature; (6) 5 days at 12°C and 5 days 24°C per 10 days, mimicking the impact of an extreme heat wave; (7) a simulated daily air temperature cycle for June in the Westerwald mountain range (minimum: 12°C, maximum: 23°C, mean: 17.4°C), mimicking the conditions in small water bodies which became disconnected from the spring due to (partial) drying-up. Sample size was 20 individuals (i.e., 2 replicate plastic boxes) per spring and treatment ($N_{\text{total}} = 980$). Snails were exposed to the respective treatment for 30 days. Every 10 days, water was renewed and the mortality rate scored. The water level was kept constant throughout the experiment by supplementing evaporated water as necessary. As mortality rates were rather low throughout (see "Results" section), the rather extreme treatment 7 was prolonged for another 36 days to check whether exposure times may have been too short to more substantially increase mortality. As above, we used 20 individuals per spring, i.e., individuals which had died during the first 30 days were replaced.

Throughout, mortality rates were scored in 8°C cold water with a binocular microscope (Olympus SZ 40). Typically, the operculum opens very fast under such conditions, indicating that snails were still alive. If snails did not open their operculum within 10 min, they were gently simulated using forceps, which typically yielded an immediate response. In case no response occurred, the snail was considered dead. Similarly, snails with a permanently open operculum were considered dead if stimulation did not yield a response.

Experiment 2: desiccation resistance

Here, we used four desiccation treatments involving exposure times without water of 2, 6, 12, and 24 h. Sample size was 10 individuals per spring and treatment ($N_{\text{total}} = 280$). For exposure, snails were individually taken out of the water after the acclimation period and gently dried using filter paper. They were then kept for the respective number of hours at 8°C and 60% relative humidity. After exposure, snails were transferred to plastic boxes filled with water at 8°C. Mortality was scored as outlined above 24 h later.

Experiment 3: pH tolerance

We here used five different pH values, namely 7.0 (control), 6.4, 5.8, 5.2, and 4.6, all at a temperature of 8°C. Sample size was 20 individuals (i.e., 2 replicate plastic boxes) per spring and treatment. Surplus individuals from the respective springs were pooled in order to get an additional population sample ($N_{\text{total}} = 400$; 4 'springs' × 20 individuals × 5 pHs). pH values were adjusted using 1 M HCl and a pH meter (Hanna Instruments, pH211). Snails were exposed to the respective treatment for 30 days. Every 10 days, water was renewed and the mortality rate scored. As mortality rates were rather low throughout (see "Results" section), all surviving snails were subsequently exposed to a more extreme pH of 3.6 for another 30 days. Snails were otherwise treated as indicated above.

Statistical analyses

The field data were first analysed in a univariate fashion using Mann–Whitney *U* tests to compare environmental parameters of (1) sampling points which were occupied or not occupied by *B. dunkeri*, and of (2) sampling points located in occupied versus unoccupied springs. In the latter approach, a spring was qualified as occupied in case *B. dunkeri* occurred at least one sampling point within the respective spring. All sampling points within the respective spring were then treated equally, no matter whether the individual point was actually occupied or not. While the first approach thus investigated differences between occupied and unoccupied individual sites, the latter investigated differences between occupied and unoccupied springs. We corrected for table-wide false discovery rates by applying a sequential Bonferroni correction. As it is not possible to account for the non-independence of the sampling points within a given spring when using *U* tests, we additionally performed general mixed models with 'spring' as random factor (see below).

Specifically, we used generalized linear models with a logit-link function and a binomial error distribution on binary data (presence, absence), for both occupied versus unoccupied sampling points and the sampling points of occupied versus unoccupied springs (see above). Models were constructed by stepwise forward inclusion of significant factors. Variation in the number of individuals per sampling point was investigated (for occupied springs only) using a stepwise forward multiple regression ($F > 1.00$ for inclusion, Ridge regression, $\lambda = 0.10$). Predictor variables in the above models included all parameters evaluated, except from salt concentration due to very low variation across sampling points (range 0–0.02%, with the value 0.01 being measured at 96 out of 131 sampling points), and acid-binding capacity due to a high correlation with conductivity ($R = 0.787$, $P < 0.001$). If applicable, analyses were performed twice using either the instant water temperature recorded during field surveys (thus using the full data set) or the standard deviation of the temperatures measured by the data loggers (available for only a subset of sampling points). Other data based on the loggers, namely mean temperature, maximum temperature, and minimum temperature, were not considered due to high correlations with the standard deviation (range of *R*-values: 0.483 to 0.790). Doing so would not change any results presented here qualitatively. Note that the standard deviation of temperature was never included in the final model, such that only the models (initially) including instant temperature are presented. The above generalized models were used for illustrative purposes only, as they do not account for the non-independence of the sampling points within a given spring.

To analyse capacity for plasticity, we used contingency tables comparing the distributions of dead and alive individuals per spring across treatments (temperature treatment, desiccation period, pH) and springs. We refrained from using alternative analyses due to the low mortality rates found. We used Statistica 8.0 (StatSoft Inc., Tulsa, OK, USA) for all statistical analyses. Throughout all mean values are given 1 ± SE.

Results

Field survey and habitat preferences

Out of the 30 springs 17 (57%) were occupied by *B. dunkeri* while 13 were not. We found on average 24 individuals per sampling point within the 10 min sampling period (range 0–188). Sixty-three (48%) out of 132 sampling points were inhabited by *B. dunkeri*. The 69 unoccupied sampling points included 17 located in occupied springs, i.e., not all sampling points in a spring harboring snails were occupied. Such unoccupied sampling points within occupied springs occurred mainly further downstream, as indicated by a substantial decrease in snail numbers with increasing distance from the crop-out (Fig. 1). The less densely populated downstream sections were characterized by higher temperatures during the vegetation period and also by a much higher temperature variation within and across days (Fig. 2).

Univariate comparisons using *U* tests among occupied and unoccupied sampling points revealed that the latter showed on average a significantly (1) higher distance from the crop-outs, in accordance with above, (2) a more disturbed, i.e., less natural, structure, (3) a larger water depth, (4) a lower pH, (5) a lower redox potential, and (6) a lower acid-binding capacity (Table 1a). Note though that differences in structure and redox potential were not significant anymore after

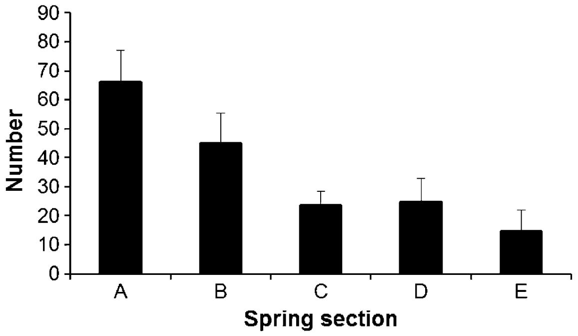

Fig. 1 Mean number (+1 SE) of *B. dunkeri* individuals in relation to the distance from the crop-out of the spring for occupied springs only ($N = 80$ sampling points). Spring sections refer to distances of 0–20 m (*A*), 30–75 m (*B*), 80–140 m (*C*), 150–230 m (*D*), and 250–450 m (*E*) from the crop-out

Bonferroni correction. General mixed models indicated that all parameters given in Table 1a but shadowing differed significantly among springs (data not shown). Otherwise, the above results could be largely confirmed with significant differences occurring for the distance to the crop-out, water depth, and acid-binding capacity, but nor for structure, redox potential, and, surprisingly, pH (data not shown). The latter was due to the fact that, within occupied springs, occupied (7.13 ± 0.05) and unoccupied (7.14 ± 0.10) sampling points had very similar pH values, while springs which were not at all inhabited by *B. dunkeri* had much lower pH values (6.47 ± 0.08; cf. Table 1b) driving the overall difference. Additionally, general mixed models indicated significant differences for stream current ($F_{1,101} = 19.9, P < 0.0001$) and oxygen concentration ($F_{1,101} = 6.9, P = 0.0099$), suggesting that occupied sites had a higher stream current but a lower oxygen concentration (Table 1a).

Comparing the sampling points located in occupied versus unoccupied springs indicated that, similar to above, unoccupied springs were characterized by a significantly (1) less natural structure, (2) lower stream current, (3) larger water depth, (4) lower pH, (5) lower redox potential, and (6) a lower acid-binding capacity (Table 1b). Differences in stream current and redox potential were not significant anymore after Bonferroni correction. General mixed models indicated that all parameters given in Table 1b, except from distance

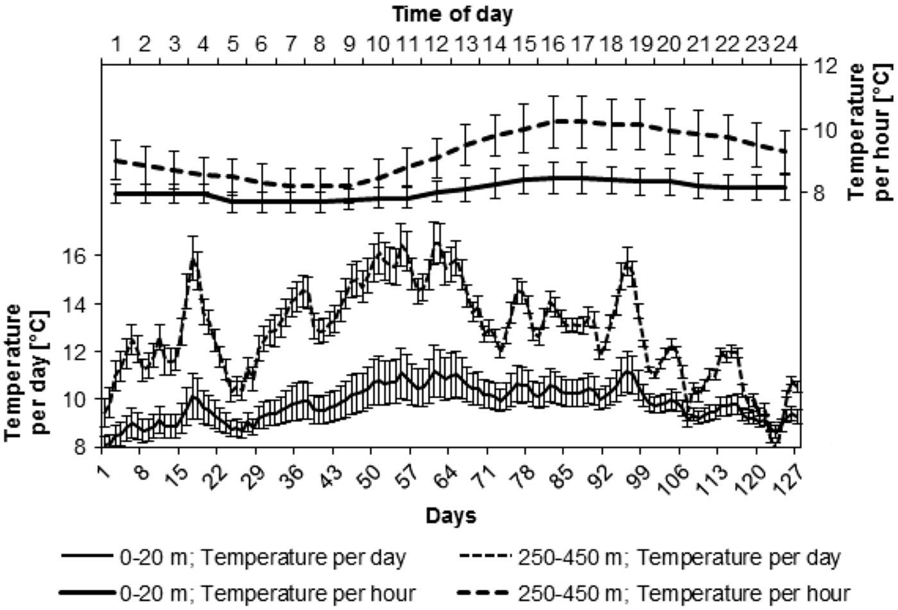

Fig. 2 Water temperature variation for a single representative day (*top*) and across the whole study period (*bottom*) for cop-outs of springs (0–20 m) and spring-fed brooks (at a distance of 250–450 m from the crop-out) in the Westerwald mountain range. Hourly temperature variation within a day is shown using the 3rd June 2013 as example (*top*). Daily temperature variation is shown for the time period between 3rd June and 7th October 2013 (*bottom*). Given are means ± 1 SE based on 6–7 data loggers each (iButton DS1923)

to crop-out, shadowing, substrate diversity, and water depth, differed significantly among springs (data not shown). All significances shown in Table 1b, including those which were not significant anymore after Bonferroni correction, could be confirmed by the general models (all P values <0.006). Additionally, significant results were found for substrate type ($F_{1,114} = 7.8$, $P = 0.0062$), temperature ($F_{1,114} = 20.2$, $P < 0.0001$), and phosphate concentration ($F_{1,114} = 5.4$, $P = 0.0223$), indicating that occupied springs tended to show substrates consisting mainly of sand/stones and combinations of different substrates, higher temperatures, and lower phosphate concentrations.

The above findings could be largely backed up by generalized linear models, used here for illustrative purposes. Regarding the comparison between occupied and unoccupied sampling points, pH, distance from crop-out, water depth, and redox potential were found to have significant effects (Table 2). Thus, a higher pH, a shorter distance to the crop-out, a lower water depth, and a higher redox potential affected snail occurrence positively (Fig. 3a–c; cf. Figure 1 and Table 1a). The equivalent analysis for spring occupation showed significantly positive effects of a higher pH and redox potential and of a more natural structure on spring occupation (Table 2; Fig. 3d; cf. Table 1b). Snail numbers within occupied springs were significantly negatively affected by the distance to the crop-out and oxygen concentration, and significantly positively by pH (Table 3). Furthermore, snail numbers tended to decrease with increasing phosphate concentration.

Capacity for plasiticity

The different thermal treatments induced low but differential mortality rates ($X_6^2 = 22.5$, $P = 0.001$), which also differed significantly among springs ($X_6^2 = 52.9, P < 0.001$; Table 4). Mortality rates were highest for the control and the diurnal temperature cycle treatments, and for individuals originating from spring 4. Exposing the snails to ongoing temperature cycles for another 36 days resulted in an overall mortality rate of still only 7.9% (S1: 5%; S2: 5%, S3: 0%, S4: 25%, S5: 10%, S6: 0%, S7: 10%). In contrast, desiccation had a much higher impact on mortality ($X_3^2 = 146.0$, $P < 0.001$), which strongly increased with increasing exposure time without water. Here, mortality rates did not differ across springs ($X_6^2 = 6.37$, $P = 0.383$; Table 5). Finally, mortality rates were also significantly affected by pH, slightly increasing with decreasing pH ($X_4^2 = 10.7$, $P = 0.031$). Snails from different springs showed similar responses to pH ($X_3^2 = 2.5$, $P = 0.471$; Table 6). Exposing the surviving snails to a more extreme pH of 3.6 for another 30 days revealed a further increase in mortality to overall 14% (spring 1: 32%, 2: 5%, 3: 7%, mix: 9%).

Discussion

Factors affecting *B. dunkeri* occurrence

Our field data suggest that *B. dunkeri* has indeed a very narrow niche space, being restricted to springs and

Table 2 Results of generalized linear models with a logit-link function and a binomial error distribution for the factors affecting sampling point or spring occupation by *B. dunkeri*

Parameter	DF	Estimate ± SE	Wald χ^2	P
Sampling point				
pH	1	−2.25 ± 0.55	16.87	**<0.0001**
Distance to crop-out	1	0.01 ± <0.01	13.27	**0.0003**
Water depth	1	0.43 ± 0.15	7.64	**0.0057**
Redox potential	1	−0.01 ± <0.01	6.66	**0.0098**
Spring				
pH	1	−2.44 ± 0.52	22.33	**<0.0001**
Redox potential	1	−0.02 ± <0.01	11.71	**0.0006**
Structure	1	−0.94 ± 0.35	7.12	**0.0076**

Models were constructed by stepwise forward inclusion of significant factors ($P < 0.05$). Significant P values are given in bold

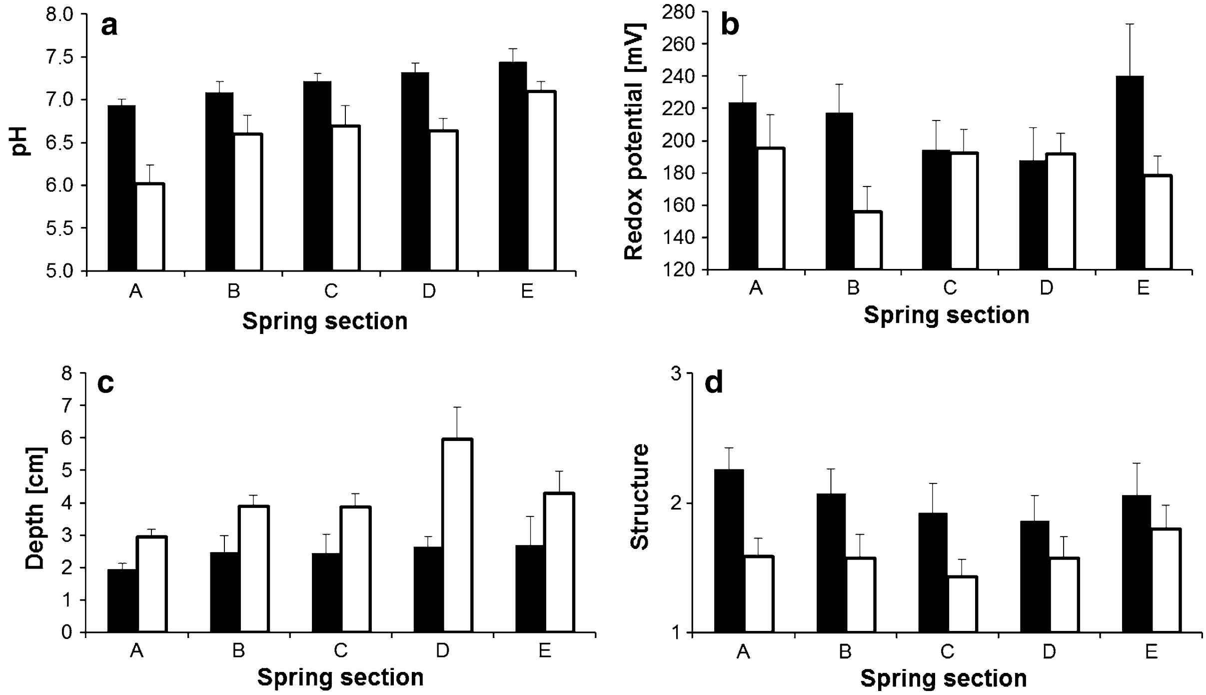

Fig. 3 Mean (+1 SE) values for pH (**a**), redox potential (**b**), and water depth (**c**) for occupied ($N = 63$) versus unoccupied ($N = 69$) sampling points, and for structure (**d**) for occupied ($N = 80$ sampling points) versus unoccupied ($N = 52$) springs. All values are given in relation to spring sections referring to the distance from the crop-out: 0–20 m (*A*), 30–75 m (*B*), 80–140 m (*C*), 150–230 m (*D*), and 250–450 m (*E*). *Black bars* occupied sampling points/springs; *open bars* unoccupied sampling points/springs

Table 3 Results of a stepwise forward multiple regression ($T > 1.00$ for inclusion, Ridge regression, lambda = 0.10) for the factors affecting the number of *B. dunkeri* individuals within occupied springs

Parameter	Beta ± SE	R^2	T	P
Distance to crop-out	−0.331 ± 0.108	0.169	−3.07	**0.0030**
Oxygen	−0.439 ± 0.128	0.223	−3.43	**0.0010**
pH	0.226 ± 0.103	0.287	2.21	**0.0304**
Phosphate	−0.185 ± 0.094	0.324	−1.97	0.0527
Conductivity	0.168 ± 0.111	0.345	1.52	0.1322
Temperature	−0.170 ± 0.120	0.358	−1.41	0.1630
Redox potential	0.127 ± 0.112	0.369	1.23	0.2630

Significant P values are given in bold. Beta: Standardised correlation coefficient; R^2: Multiple coefficient of determination

adjacent brooks. Given that water temperature and especially its variability changes rapidly downstream in the spring-fed brooks (Fig. 2), we assumed temperature to be the decisive factor restricting *B. dunkeri* to thermally stable, permanently cold environments. However, we were not able to find a significant impact of temperature per se on either site occupancy or snail numbers, which is also supported by our experimental data (see below). Instead, snail occurrence and abundance were mainly affected by the distance to the spring crop-out, water depth, water pH, and concomitantly acid-binding capacity. Additionally, there was evidence that spring structure, substrate type, stream current, water redox potential, oxygen concentration

Table 4 Mortality rates (%) of *Bythinella dunkeri* from seven different springs across thermal treatments

Spring	8°C	12°C	8/12°C	8/18°C	12/24°C[a]	12/24°C[b]	Cycle	Total_S
1	0	5	0	0	0	0	5	1.4
2	0	0	0	0	0	0	0	0.0
3	0	0	0	0	5	0	0	0.7
4	15	0	0	5	0	20	45	12.1
5	35	0	5	0	0	5	0	6.4
6	0	0	0	0	5	5	0	1.4
7	0	0	0	5	0	0	0	0.7
Total_T	7.1	0.7	0.7	1.4	1.4	4.3	7.1	

Presented data are pooled across two replicates per treatment. 8°C: permanent temperature of 8°C (control); 12°C: permanent temperature of 12°C; 8/12°C: 12 h at 8°C and 12 h at 12°C per day; 8/18°C: 5 days at 8°C and 5 days at 18°C per 10 days; 12/24°C[a]: 12 h at 12°C and 12 h at 24°C per day; 12/24°C[b]: 5 days at 12°C and 5 days 24°C per 10 days; Cycle: Exposure to diurnal air temperature cycles. Sample size was 20 per spring and treatment throughout ($N_{\text{total}} = 980$). In addition we present the overall mortality rate (%) per treatment (bottom, Total_T) and per spring (right column, Total_S)

Table 5 Mortality rates (%) of *B. dunkeri* from seven different springs across four desiccation treatments, differing in exposure time without water (2, 6, 12, and 24 h)

Spring	2 h	6 h	12 h	24 h	Total_S
1	0	20	60	70	37.5
2	0	40	100	80	55.0
3	0	20	100	80	50.0
4	0	70	80	100	62.5
5	0	40	80	70	47.5
6	0	20	90	80	47.5
7	0	30	100	100	57.5
Total_T	0.0	34.3	87.1	82.9	

Sample size was 10 per spring and treatment throughout ($N_{total} = 280$). In addition we present the overall mortality rate (%) per treatment (bottom, Total_T) and per spring (right column, Total_S)

and phosphate concentration may affect snail occurrence. Thus, *B. dunkeri* habitats comprise unpolluted springs with a largely undisturbed structure, a neutral pH and a high acid-binding capacity, confirming our first prediction except with regard to the impact of temperature. These findings may suggest that factors other than the thermal conditions may play the decisive role for restricting *B. dunkeri* to spring habitats. Potential factors include an altered species community structure, which typically changes rapidly with increasing distance to the crop-out (Clenaghan et al., 1998), and associated changes in competition, predation, and/or parasitism (Lock & Reynoldson, 1976).

Table 6 Mortality rates (%) of *B. dunkeri* from three different springs across water pH values ranging from 4.6 to 7.0

Spring	pH 4.6	pH 5.2	pH 5.8	pH 6.4	pH 7.0	Total_S
1	10	0	0	0	0	2.0
2	0	5	0	0	0	1.0
3	10	5	0	5	0	4.0
Mix	10	5	5	0	0	4.0
Total_T	4.8	2.4	0.8	0.8	0.0	

Presented data are pooled across two replicates per treatment. Surplus individuals from the three springs were mixed to generate an additional data set. Sample size was 20 per spring and treatment throughout ($N_{\text{total}} = 400$). In addition we present the overall mortality rate (%) per treatment (bottom, Total_T) and per spring (right column, Total_S)

The fact that pH and acid-binding capacity had positive effects on the occurrence of *B. dunkeri* is not surprising, as a low pH may interfere with shell formation in water molluscs (Hunter, 1990; Spyra, 2010). Moreover, water with a low pH may dissolve heavy metals from the soil, potentially reaching toxic levels (Muniz, 1991), and may disrupt the functioning of the sodium potassium pump (Vinogradov et al., 1993). A high redox potential indicates oxygen-rich water of a very good quality, a lack of reducing compounds and organic substances, which may explain its positive effects on *B. dunkeri* occurrence. Note in this context, the detrimental effects of higher phosphate concentrations indicating eutrophication. Also, snails preferred more natural structures suggesting a generally high sensitivity to habitat degradation. A higher stream current may indicate higher discharge rates, and thus a reduced risk of drying-up during droughts. Alternatively, it may affect microbial biofilms and thus food availability (Battin et al., 2003). Regarding substrate type, our results indicate a slight preference for sand/stones and combinations of different substrates, which may be important for food availability (Reiss, 2011) and for shelter (Haase, 2003).

Capacity for plasticity of *B. dunkeri*

In line with the findings from the field, our laboratory experiments suggest that *B. dunkeri* may not be adapted to any specific thermal regime. Surprisingly, the species was able to survive very high and strongly fluctuating thermal regimes for extended periods of time, with essentially no effects on mortality rate. However, the same was true for pH values, which did have a strong impact on snail occurrence in nature. Therefore, our treatments may not have been imposed on the animals long enough to yield a more substantial response, although exposure times ranged between 30 and 66 days. Alternatively, stressful thermal conditions and pH values may not interfere in the first place with survival in the adult stage, but rather with reproduction which we could not test here. Detrimental effects of fluctuating temperatures have, for instance, been shown for different fish species (McDonald et al., 2007). However, Oswald et al. (1991) reported that *B. dunkeri* is well able to reproduce at high temperatures, and Schindler (1988) suggested that a low pH is not really critical for the species. In any case, our laboratory and field data suggest that temperature and its variation may not be the decisive factor limiting the distribution of *B. dunkeri*. Based on the relatively high tolerances against pH and thermal variation, the species may be less sensitive to environmental change than expected for such a habitat specialist.

In contrast to pH and temperature, *B. dunkeri* was highly susceptible to desiccation, partly confirming our second prediction. Substantial mortality occurred after 6 h without water, and the vast majority of animals was killed after 12 h. Thus, *B. dunkeri* appears to be much more sensitive to desiccation than other operculate freshwater snails (van Leeuwen & van der Velde, 2012; Havel et al., 2014). Note here that other studies assumed a relatively high desiccation resistance for adults in the genus *Bythinella* (Falniowski, 1987; Szarowska, 2000) in contrast to the eggs (Szarowska, 1996). However, low desiccation resistance might be an important determinant of the species vulnerability to climate change, as less regular precipitation may result in a reduction of groundwater recharge and consequently spring discharge (Eckhardt & Ulbrich, 2003). Indeed the species does not occur in springs which occasionally dry up during summer, at least in the study area (KF, personal observation).

Conclusions

Without any doubt *B. dunkeri* has a narrow niche space, being a specialist of largely undisturbed springs. However, the species' quick disappearance downstream spring-fed brooks remain enigmatic, despite using a combined approach entailing field work and laboratory experiments. Regarding capacity for plasticity toward temperature, we found a little reason for concern in this purportedly 'cold-stenothermic' species. As no other parameter examined here is likely to correlate strongly with the distance to the crop-out and may thus explain the species' disappearance, we believe that biotic interactions such as food availability, competition, predation, and/or parasitism may play a crucial role (Lock & Reynoldson 1976; Clenaghan et al., 1998). However, neither potential competitors nor predators were detected in meaningful numbers during field work, regardless of whether a specific location was occupied or not. Another possibility is that factors of critical importance were not covered, for instance specific ions such as Ca^{2+}, Mg^{2+}, Na^{+}, and K^{+} which may have important impacts on aquatic snails (Dussart, 1979). Regarding low pH values, *B. dunkeri* was clearly negatively affected in the field but only marginally so in laboratory experiments. The vulnerability to low pH may pose a more substantial problem in the future due to acidification caused by pollution or forestry (preference for conifers; Schindler, 1988). The most important threat discovered in our study though is a low desiccation resistance, which may strongly affect the species' distribution if yearly precipitation or its distribution changes substantially, which may cause extended drought periods. To what extent a recolonization of springs is possible after drying-up is unclear at the moment, though recolonization events were assumed to occur in other *Bythinella* species (Falniowski et al., 2009). Passive transportation by insects and birds is certainly common in minute water snails (Rees, 1965; Haase et al., 2010; van Leeuwen & van der Velde, 2012). To sum up, although changes in thermal conditions may not directly affect the future survival of this supposedly stenothermic snail species, this does not mean that the species is not vulnerable to environmental change. However, increased threats under changing environmental conditions seem to arise from a factor other than the most obvious one. Our study thus exemplifies the value of in-depth investigations into the habitat preferences and capacity for plasticity of specialist species in order to allow for better predictions regarding the fate of such species under environmental change.

Acknowledgments This study was in part financially supported by the Federal Agency for Nature Conservation (BfN; UFOPLAN 2011, FKZ3511860200). We thank the Struktur- und Genehmigungsdirektion Nord (SGD Nord), Department for Nature Conservation, for granting permission to pursue this study and two anonymous reviewers for helpful comments on the manuscript. MK is associated doctoral researcher of the research training group RESPONSE funded by the German Research Council (DFG GRK2010).

References

Battin, T. J., L. A. Kaplan, J. Denis Newbold & C. M. E. Hansen, 2003. Contributions of microbial biofilms to ecosystem processes in stream mesocosms. Nature 426: 439–442.

Benke, M., M. Brändle, C. Albrecht & T. Wilke, 2009. Pleistocene phylogeography and phylogenetic concordance in cold-adapted spring snails (*Bythinella* spp.). Molecular Ecology 18: 890–903.

Benke, M., M. Brändle, C. Albrecht & T. Wilke, 2011. Patterns of freshwater biodiversity in Europe: lessons from the spring snail genus *Bythinella*. Journal of Biogeography 38: 2021–2032.

Boag, D. A., 1986. Dispersal in pond snails: potential role of waterfowl. Canadian Journal of Zoology 64: 904–909.

Bradshaw, W. E. & C. M. Holzapfel, 2006. Evolutionary response to rapid climate change. Science 312: 1477–1478.

Brändle, M., I. Westermann & R. Brandl, 2005. Gene flow between populations of two invertebrates in springs. Freshwater Biology 50: 1–9.

Brown, J. H., 1984. On the relationship between abundance and distribution of species. American Naturalist 124: 255–279.

Cantonati, M., R. Gerecke & E. Bertuzzi, 2006. Springs of the Alps–sensitive ecosystems to environmental change: from biodiversity assessments to long-term studies. Hydrobiologia 562: 59–96.

Clenaghan, C., P. S. Giller, J. O'halloran & R. Hernan, 1998. Stream macroinvertebrate communities in a conifer-afforested catchment in Ireland: relationships to physicochemical and biotic factors. Freshwater Biology 40: 175–193.

Cushman, S. A., 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biological conservation 128: 231–240.

Delicado, D., A. Machordom & M. A. Ramos, 2014. Vicariant versus dispersal processes in the settlement of *Pseudamnicola* (Caenogastropoda, Hydrobiidae) in the Mediterranean Balearic Islands. Zoological Journal of the Linnean Society 171: 38–71.

Di Sabatino, A., B. Cicolani & R. Gerecke, 2003. Biodiversity and distribution of water mites (Acari, Hydrachnidia) in spring habitats. Freshwater Biology 48: 2163–2173.

Dillon, R. T., 2000. The Ecology of Freshwater Molluscs. Cambridge University Press, Cambridge.

Dussart, G. B. J., 1979. Life cycles and distribution of the aquatic gastropod molluscs *Bithynia tentaculata* (L.), *Gyraulus albus* (Muller), *Planorbis planorbis* (L.) and *Lymnaea peregra* (Muller) in relation to water chemistry. Hydrobiologia 67: 223–239.

Eckhardt, K. & U. Ulbrich, 2003. Potential impacts of climate change on groundwater recharge and streamflow in a central European low mountain range. Journal of Hydrology 284: 244–252.

Falniowski, A., 1987. Hydrobioidea of Poland (Prosobranchia: Gastropoda). Folia Malacol 1: 1–122.

Falniowski, A. & M. Szarowska, 2011. Radiation and Phylogeography in a Spring Snail *Bythinella* (Mollusca: Gastropoda: Rissooidea) in Continental Greece. Annales Zoologici Fennici 48: 67–90.

Falniowski, A., M. Szarowska & I. Sirbu, 2009. *Bythinella* Moquin-Tandon, 1856 (Gastropoda: Rissooidea: Bythinellidae) in Romania: species richness in a glacial refugium. Journal of Natural History 43: 2955–2973.

Figuerola, J. & A. J. Green, 2002. Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. Freshwater biology 47: 483–494.

Fox, L. R. & P. A. Morrow, 1981. Specialization: species property or local phenomenon. Science 211: 887–893.

Gaston, K. J., T. M. Blackburn & J. H. Lawton, 1997. Interspecific abundance-range size relationships: an appraisal of mechanisms. Journal of Animal Ecology 66: 579–601.

Haase, M., 2003. Clinal variation in shell morphology of the freshwater gastropod *Potamopyrgus antipodarum* along two-hill country streams in New Zealand. Journal of the Royal Society of New Zealand 33: 549–560.

Haase, M., M. D. Naser & T. Wilke, 2010. *Ecrobia grimmi* in brackish Lake Sawa, Iraq: indirect evidence for long-distance dispersal of hydrobiid gastropods (Caenogastropoda: Rissooidea) by birds. Journal of Molluscan Studies 76: 101–105.

Havel, J. E., L. A. Bruckerhoff, M. A. Funkhouser & A. R. Gemberling, 2014. Resistance to desiccation in aquatic invasive snails and implications for their overland dispersal. Hydrobiologia 741: 89–100.

Hoffsten, P.-O. & B. Malmqvist, 2000. The macroinvertebrate fauna and hydrogeology of springs in central Sweden. Hydrobiologia 436: 91–104.

Hunter, R. D., 1990. Effects of low pH and low calcium concentration on the pulmonate snail *Planorbella trivolvis*: a laboratory study. Canadian Journal of Zoology 68: 1578–1583.

Illies, J., 1978. Limnofauna europaea. Gustav Fischer Verlag, Stuttgart.

Johnson, C. N., 1998. Species extinction and the relationship between distribution and abundance. Nature 394: 272–274.

Jungbluth, J. H., 1973. Zur Verbreitung und Ökologie von *Bythinella dunkeri* und *compressa* (Frauenfeld 1856). Verhandlungen des Internationalen Verein Limnologie Part 3: 1576–1585.

Jungbluth, J. H. & D. Knorre, 2009. Rote Liste der Binnenmollusken [Schnecken (Gastropoda) und Muscheln (Bivalvia)] in Deutschland: - 6. Fassung. Mitteillungen der deutschen malakozoologischen Gesellschaft 81: 1–28.

Lindegaard, C., K. P. Brodersen, P. Wiberg-Larsen & J. Skriver, 1998. Multivariate analyses of macrofaunal communities in Danish springs and springbrooks. In Botosaneanu, L. (ed.), Studies in Crenobiology: The Biology of Springs and Springbrooks. Backhuys Publishers, Leiden: 201–210.

Lock, M. A. & T. B. Reynoldson, 1976. The role of interspecific competition in the distribution of two stream dwelling triclads, *Crenobia alpina* (Dana) and *Polycelis felina* (Dalyell), in North Wales. The Journal of Animal Ecology 45: 581–592.

McCabe, D. J., 1998. Biological communities in springbrooks. In Botosaneanu, L. (ed.), Studies in Crenobiology. The Biology of Springs and Springbrooks. Backhuys Publishers, Leiden: 221–228.

McDonald, D. L., T. H. Bonner, E. L. Oborny & T. M. Brandt, 2007. Effects of fluctuating temperatures and gill parasites on reproduction of the fountain darter, *Etheostoma fonticola*. Journal of Freshwater Ecology 22: 311–318.

Muniz, I. P., 1991. Freshwater acidification: its effects on species and communities of freshwater microbes, plants and animals. Proceedings of the Royal Society of Edinburgh 97: 227–254.

Oswald, D., A. Kureck & D. Neumann, 1991. Populations dynamik, Temperaturtoleranz und Ernährung der Quellschnecke *Bythinella dunkeri* (Frauenfeld 1856). Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere 118: 65–78.

Parmesan, C. & G. Yohe, 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37–42.

Ponder, W. F. & D. J. Colgan, 2002. What makes a narrow-range taxon? Insights from Australian freshwater snails. Invertebrate Systematics 16: 571–582.

Rees, W. J., 1965. The aerial dispersal of Mollusca. Malacological Society of London 36: 269–282.

Reiss, M., 2011. Substratpräferenz und Mikrohabitat-Fauna-Beziehung im Eukrenal von Quellgewässern. Dissertation, Philipps-Universität, Marburg.

Ricklefs, R. E., 2010. Evolutionary diversification, coevolution between populations and their antagonists, and the filling of niche space. Proceedings of the National Academy of Sciences of the United States of America 107: 1265–1272.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson & A. Kinzig, 2000. Global biodiversity scenarios for the year 2100. Science 287: 1770–1774.

Schindler, D. W., 1988. Effects of acid rain on freshwater ecosystems. Science 239: 149–157.

Slatyer, R. A., M. Hirst & J. P. Sexton, 2013. Niche breadth predicts geographical range size: a general ecological pattern. Ecology letters 16: 1104–1114.

Spyra, A., 2010. Environmental factors influencing the occurrence of freshwater snails in woodland water bodies. Biologia 65: 697–703.

Steingötter, K., 2005. Geologie von Rheinland-Pfalz. E. Schweizerbart'sche Verlagsbuchhandlung (Nägele u. Obermille), Stuttgart.

Sturm, R., 2005. Modelling optimum ranges of selected environmental variables for habitats colonized by the spring snail *Bythinella austriaca* (v. Frauenfeld, 1857)(Gastropoda, Prosobranchia). Malak. Abh 23: 67–76.

Swihart, R. K., T. M. Gehring, M. B. Kolozsvary & T. E. Nupp, 2002. Responses of 'resistant́ vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. Diversity and Distributions 9: 1–18.

Szarowska, M., 1996. The egg capsules of *Bythinella austriaca* (Frauenfeld, 1856) with observations on the veliger and embryonic shell. Journal of Molluscan Studies 62: 546–549.

Szarowska, M., 2000. Environmental threats and stability of *Bythinella* populations in SouthPoland (Gastropoda: Prosobranchia: Hydrobioidea). Malakol Ab Staat Mus Tier Dresden 20: 93–98.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. De Siqueira, A. Grainger & L. Hannah, 2004. Extinction risk from climate change. Nature 427: 145–148.

Thuiller, W., S. Lavorel & M. B. Araujo, 2005. Niche properties and geographical extent as predictors of species sensitivity to climate change. Global Ecology and Biogeography 14: 347–357.

Van Leeuwen, C. H. A. & G. van der Velde, 2012. Prerequisites for flying snails: external transport potential of aquatic snails by waterbirds. Freshwater Science 31: 963–972.

Vinogradov, G. A., N. F. Smirnova, V. A. Sokolov & A. A. Bruznitsky, 1993. Influence of chemical composition of the water on the mollusk *Dreissena polymorpha*. In Nalepa, T. F. & D. W. Schloesser (eds), Zebra Mussels: Biology, Impacts, and Control. Lewis Publishers Inc., Boca Raton, FL: 283–294.

Wetterdienst, D., 2014. Klimadaten für Messstationen in Deutschland. Offenbach.

Wilke, T., M. Haase, R. Hershler, H.-P. Liu, B. Misof & W. Ponder, 2013. Pushing short DNA fragments to the limit: Phylogenetic relationships of "hydrobioid" gastropods (Caenogastropoda: Rissooidea). Molecular phylogenetics and evolution 66: 715–736.