

Modelling optimum ranges of selected environmental variables for habitats colonized by the spring snail *Bythinella austriaca* (v. Frauenfeld, 1857) (Gastropoda, Prosobranchia)

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Abstract. Habitat requirements of the central European spring snail *Bythinella austriaca* (v. Frauenfeld, 1857) were simulated using a) logistic regression and b) generalized additive models (GAM). With this mathematical approaches, the probability of occurrence $p(x)$ of a species is predicted as a function of various environmental variables. For 10 selected environmental variables, maximum probabilities of occurrence (p_{max}), optimum habitat ranges (r_{opt}), and maximum ranges of occurrence (r_{occ}) were computed. Goodness-of-fit of the generated regression functions was tested by calculating the reduction in deviance (D), describing the relationship between the deviance of the null model with only a constant term and that of the fitted model. For both regression models, the correlation between probability of occurrence and environmental variable was expressed by bell-shaped regression curves. Values of D ranging from 6.5 to 14.5 for logistic regression and from 36.9 to 63.4 for GAM underlined the importance of all selected parameters concerning the distribution of *Bythinella*.

Kurzfassung. Modellierung optimaler Bereiche von ausgewählten Umweltvariablen für Habitate der Quellschnecke *Bythinella austriaca* (v. Frauenfeld, 1857) (Gastropoda, Prosobranchia). Habitatansprüche der mitteleuropäischen Quellschnecke *Bythinella austriaca* (v. Frauenfeld, 1857) wurden unter Verwendung a) der logistischen Regression und b) generalisierter additiver Modelle (GAM) simuliert. Bei diesen mathematischen Näherungen wird die Auftretswahrscheinlichkeit $p(x)$ einer Art als Funktion verschiedener Umweltvariablen vorhergesagt. Für 10 ausgewählte Variablen wurden maximale Auftretswahrscheinlichkeiten (p_{max}), optimale Bereiche (r_{opt}) und maximale Bereiche des Auftretens der Spezies (r_{occ}) ermittelt. Die Anpassungsgüte der erzeugten Regressionsfunktionen wurde durch Berechnung des Parameters D (reduction in deviance) ermittelt. Für beide Regressionsmodelle konnte die Korrelation zwischen $p(x)$ und x in Form von glockenförmigen Regressionskurven zum Ausdruck gebracht werden. Die Werte für D reichten von 6,5 bis 14,5 (logistische Regression) bzw. von 36,9 bis 63,4 (GAM) und unterstrichen damit die Wichtigkeit der gewählten Parameter in Bezug auf die Verbreitung von *Bythinella*.

Key words. Logistic regression, GAM, habitat model, probability of occurrence, *Bythinella austriaca*.

Introduction

Nowadays, the role of freshwater molluscs as bioindicators is a largely accepted fundamental in aquatic ecology. Generally, the diversity of an aquatic mollusc community is dependent upon physical and chemical parameters and thus may be evaluated as a temporary and locally limited specificity of an ecosystem (e.g. PIP 1987, FALKNER 1990, BAADE 1993). Among aquatic gastropods and bivalvs, specific limits of tolerance for biotic and abiotic factors are subject to remarkable variabilities, therefore enabling a distinction between more generalistic and highly specialized organisms (e.g. GLÖER & MEIER-BROOK 2003). Representatives of the second category show a quick reaction to any changes of their environment, which, for instance, significantly enhances their value as indicators for the water quality. Knowledge of habitat requirements of such species provides useful information for both water quality management (STATZNER & SPERLING 1993) and restoration projects (OSBORNE et al. 1993). Despite very comprehensive distribution data collected for most central European freshwater molluscs (see overviews in GLÖER & MEIER-BROOK 2003, TURNER et al. 1998), optimum habitat ranges of single species have not been explored in detail until now.

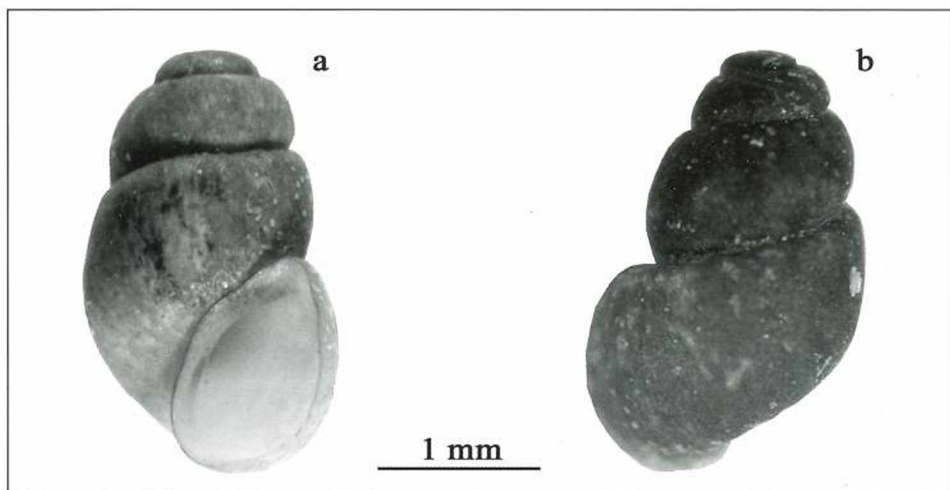


Fig. 1. Shell of the central European spring snail *Bythinella austriaca* (v. Frauenfeld, 1857). a) Front view, b) Back view.

Regression models are useful tools to study respective demands of organisms on their habitats (HOSMER & LEMESHOW 1989). As a more specific approach, regression models predicting the probability of occurrence of an organism as a function of one or more independent environmental variables (JONGMAN et al. 1987, HASTIE & TIBSHIRANI 1990, PEETERS & GARDENIERS 1998) have found a wide application in ecological sciences. While in the 1980s and the early 1990s these mathematical methods have preferentially been used for ecological investigations of macrophytes (e.g. ODLAND et al. 1995) and freshwater diatoms (TER BRAAK & VAN DAM 1989), in the last years the techniques have also excited increasing interest in the field of freshwater animal ecology (e.g. EYRE et al. 1993, PEETERS & GARDENIERS 1998, GROGER 2000, FIELD et al. 2002, YSEBAERT et al. 2002).

In the study presented here, information on the ecology of aquatic molluscs colonizing our home waters was tried to be enlarged in part by modelling the habitat requirements of the highly specialized spring snail *Bythinella austriaca* (v. Frauenfeld, 1857). For fulfilling this aim successfully, two different regression methods were applied to published data sets including both information on the distribution of freshwater molluscs in Austria and analyses of diverse physical and chemical water parameters within the colonized ecosystems. To evaluate the validity of the approaches, results of the generated models were finally compared with respective data of own field investigations.

Material and methods

Brief characteristization of *Bythinella austriaca* and available malacological data. As outlined in the overview of GLÖER & MEIER BROOK (2003), *Bythinella austriaca* represents a small gastropod species (shell height: 2.7 mm, shell width: 1.5 mm, Fig. 1) with rather limited geographic dispersal. It mainly occurs in the limestone formation of the Northern Alps East of Munich and lives in small running waters with constant temperature and high water quality. In Austria, the species was recorded at 237 of 2460 published sample points until now. All malacological data described in the literature were included into the model approach of the present study. At the sampled sites, measurement of physical and chemical water parameters was not complete in most cases, so that only ten variables could be considered for regression analysis (Tab. 1). The selected parameters, however, provide useful information on the ecological demands of *Bythinella austriaca*.

Tab. 1. Environmental parameters presented in the study with number of observations, median, minimum, and maximum values.

environmental variable		no. of observations	median	minimum	maximum
temperature	°C	2384	11.5	3.0	27.2
pH	--	1874	7.5	4.2	11.5
electric conductivity	μS cm ⁻¹	1158	341	45	952
oxygen content	mg L ⁻¹	784	9.6	4.5	18.8
total hardness	mg L ⁻¹	658	182.4	20.6	424.8
depth	cm	148	17.2	0.0	500.0
nitrate content	mg L ⁻¹	624	2.3	0.0	26.6
altitude	msm	2460	542.0	272.0	1720.0
BOD ₅	mg L ⁻¹	547	1.7	0.0	10.8
current velocity	cm s ⁻¹	278	48.5	0.0	243.0

Regression analysis. In the following section, the main characteristics of the regression methods used in this contribution are described briefly. For more detailed information, the interested reader is referred to the comprehensive overviews of TER BRAAK & LOOMAN (1986), HOSMER & LEMESHOW (1989), HASTIE & TIBSHIRANI (1990), PEETERS & GARDENIERS (1998), and HEEGAARD (2002). Logistic regression enables the analysis of the relationship between a binary response variable and one or more independent parameters. A specific case of this procedure is represented by the 'presence/absence response curve' introduced by TER BRAAK & LOOMAN (1986), where the probability of a species occurring at a sample point, $p(x)$, is expressed as function of an analyzed environmental parameter x . Generally, $p(x)$ can be written as

$$p(x) = \frac{e^{(\beta_0 + \beta_1 x + \beta_2 x^2)}}{1 + e^{(\beta_0 + \beta_1 x + \beta_2 x^2)}} \quad (1)$$

where β_0 , β_1 , and β_2 denote the regression coefficients with β_0 as constant term. For the case $\beta_2 \neq 0$, the function described by equation (1) is symmetrical and bell-shaped ('Gaussian logit curve'), whereas for the case $\beta_2 = 0$, $p(x)$ performs a sigmoidal increase or decrease. According to JONGMAN et al. (1987), the optimum range of an environmental variable may be expressed by two parameters u and t , which are estimated in the following way:

$$u = \frac{-\beta_1}{\sqrt{-2\beta_2}} \quad (2)$$

$$t = \frac{1}{\sqrt{-2\beta_2}} \quad (3)$$

The parameter u marks the position of the maximum of the probability curve, p_{max} , while the factor t (tolerance) describes the range of the independent variable between the turning points of the function ($p(x)'' = 0$). Within this interval, the probability divided by the maximum

Tab. 2. Results of a) logistic regression (generalized linear models) and b) generalized additive models (GAM). Data of the parametric approach include regression coefficients β_0 , β_1 , and β_2 , reduction in deviance D , x-position of the maximum probability of occurrence x_{max} , optimum range of occurrence r_{opt} , and total range of occurrence r_{occ} , while GAM results include regression coefficients and related values for D .

environmental variable	Logistic Regression (GLM)									
	β_0	β_1	β_2	D	x_{max}	r_{opt}	r_{occ}	const.	lin.	D
temperature	-10.400	2.0040	-0.0945	13.08	10.60	8.30–12.90	3.46–17.75	-0.400	0.043	54.020
pH	-180.520	47.4800	-3.1250	14.52	7.60	7.20–8.00	6.41–8.79	2.287	-0.273	61.850
electric conductivity	-16.600	0.0727	-0.00008	6.48	454	375–533	217–692	-2.098	0.007	49.750
oxygen content	-35.864	6.6520	-0.3120	8.04	10.66	9.39–11.93	6.99–14.32	-0.143	0.010	61.690
total hardness	-10.420	0.0826	-0.00017	8.14	243	189–297	86–400	-0.900	0.008	51.170
depth	-0.700	0.0920	-0.0026	6.89	17.69	3.82–31.56	0*–60.25	0.230	-0.005	36.970
nitrate content	-0.200	0.5200	-0.2550	8.57	1.01	0*–2.42	0*–5.29	-0.023	0.106	58.940
altitude	-4.833	0.0136	-0.0000098	13.50	693	468–920	0*–1366	0.271	-0.0004	63.420
BOD5	-0.448	1.2500	-0.5000	6.68	1.25	0.25–2.25	0*–4.39	0.347	-0.115	48.970
current velocity	-2.433	0.0584	-0.00036	11.95	81	42–118	0*–193	-0.807	0.009	52.120

probability ($p(x)/p_{max}$) does usually not fall below a value of 0.75 (PEETERS & GARDENIERS 1998). Statistical significance of the regression coefficients β_1 and β_2 was determined by application of the likelihood ratio test (HOSMER & LEMESHOW 1989, TREXLER & TRAVIS 1993), where the predictive power between normal regression and the null model (β_1 and $\beta_2 = 0$) is compared. Parameters are excluded, if no differences are noticeable.

An alternative to logistic regression is given by the non-parametric generalized additive models (GAM). Within this approach, probability of occurrence $p(x)$ is expressed as:

$$p(x) = \frac{e^{[s_0 + s_1(x)]}}{1 + e^{[s_0 + s_1(x)]}}, \quad (4)$$

where s_0 and $s_1(x)$ denote so-called smooth functions which may be estimated in different ways (HASTIE & TIBSHIRANI 1990). In the work presented here, spline smooth (YEE & MITCHELL 1991) was applied.

The goodness-of-fit of the regression model was estimated by computing the reduction in deviance, D , according to the equation

$$D = (1 - \frac{D_1}{D_0}) 100 \% \quad (5)$$

where D_1 denotes the deviance of the fitted model and D_0 the deviance of the null model (PEETERS & GARDENIERS 1998). D_0 is analogous to the sum of squares of a linear regression line fitted through the data points, while D_1 is analogous to the residual sum of squares in linear regression. High values for D , indicating a good fit of the presence/absence data by the regression model, result from low values for D_1 and vice versa.

Analysis of the published malacological data was performed in the way that presence (= 1) or absence (= 0) of *Bythinella austriaca* was plotted against each of the considered environmental

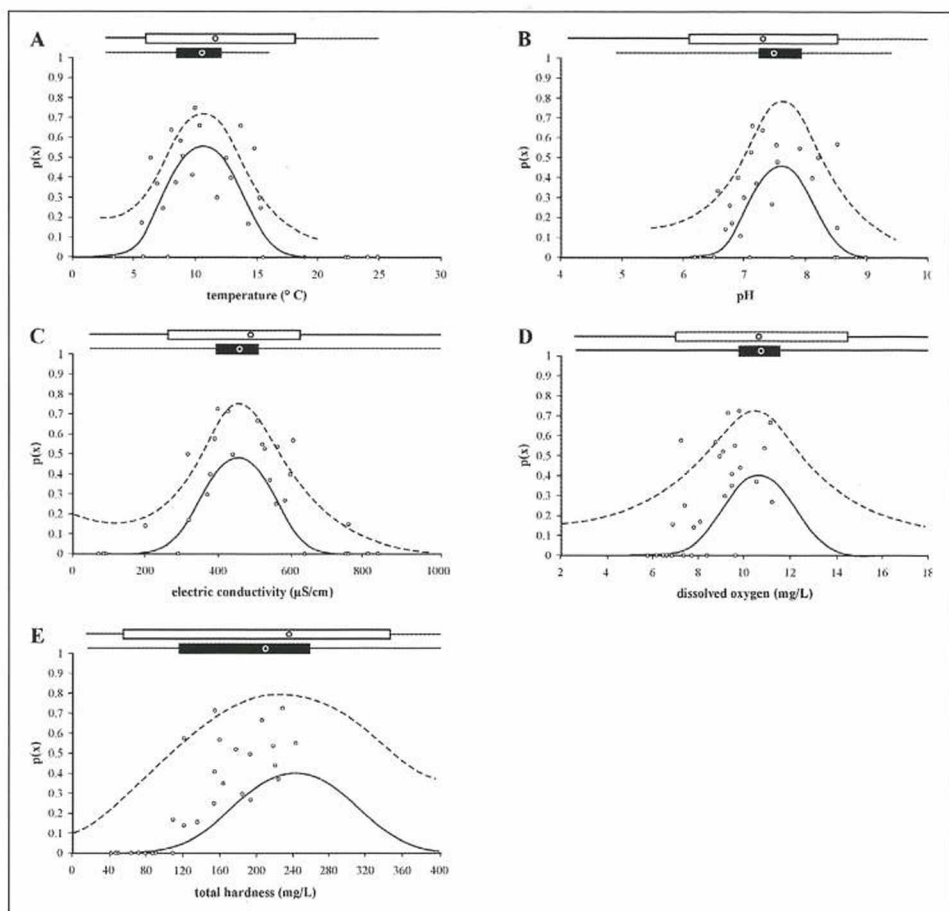


Fig. 2. Probability of occurrence of *B. austriaca* as a function of a) temperature, b) pH, c) electric conductivity, d) content of dissolved oxygen, and e) total water hardness. Circles represent probabilities of occurrence of the species derived from own field studies (STURM 1998, STURM 2000). Box plots on the top of the graphs show distributions of presence (black) and absence data (white) of *Bythinella*. Each box plot includes maximum and minimum values, first and third quartiles as well as the mean value (circle).

variables, respectively. The regression models (i.e., probability curves) were constructed by using macro-driven spreadsheets programmed in MS-Excel[®] as well as Statsoft Statistica[®]. Estimation of the regression coefficients β_0 , β_1 , and β_2 for the Gaussian logit curve was carried out according to the maximum likelihood principle (HOSMER & LEMESHOW 1989). Parameters u , t , and D were calculated automatically to determine optimum habitat ranges for a specific independent variable and the quality of the fitted curves.

Results

Table 2 provides main results of logistic regression and GAM for 10 environmental variables. Concerning the logistic model, besides the regression coefficients β_0 , β_1 , and β_2 , the reduction in deviance (D), the position of the maximum probability of occurrence (x_{\max}), the optimum

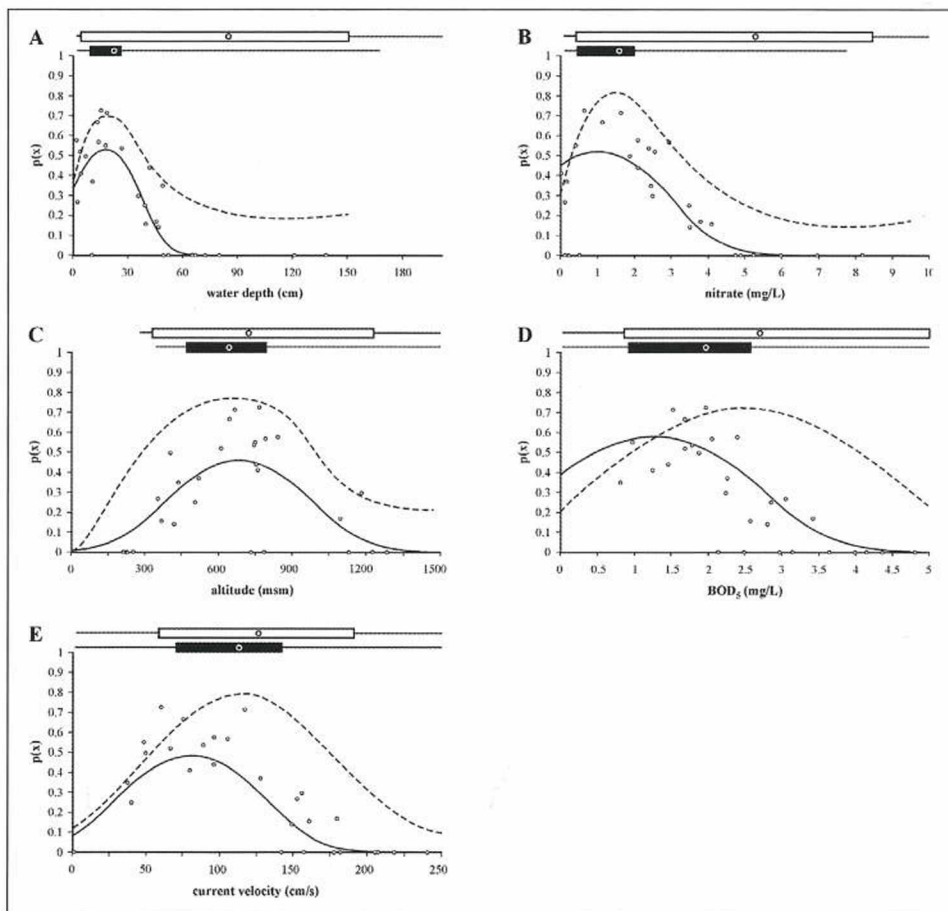


Fig. 3. Probability of occurrence of *B. austriaca* as a function of a) water depth, b) content of nitrate, c) altitude of the sampled site, d) biological oxygen demand after 5 days (BOD_5), and e) current velocity. Circles represent probabilities of occurrence of the species derived from own field studies (STURM 1998, STURM 2000). Box plots on the top of the graphs show distributions of presence (black) and absence (white) of *Bythinella*. Each box plot includes maximum and minimum values, first and third quartiles as well as the mean value (circle).

range of the studied variable (r_{opt} ; $p(x)/p_{max} \geq 0.75$), and the total range of occurrence (r_{occ} ; $p(x) > 0.01$) are listed. Regarding the non-parametric approach, constant and linear regression coefficients as well as the related values for D are presented. In figures 2 and 3, the regression curves obtained from the logistic procedure (solid lines) and the GAM procedure (dashed lines) are plotted within relevant intervals together with data from own field studies (STURM 1998, 2000), giving an estimate for the validity of the respective model. For logistic regression, the computed regression coefficient β_2 was significantly different from zero ($p < 0.01$) for all investigated environmental variables, therefore resulting in symmetrical, bell-shaped regression curves (Figs. 2, 3). As listed in table 2, reductions in deviance generally range from 6 to 15, indicating a fair approximation of the ecological data by the regression curves. Highest values for D were obtained for temperature, pH, altitude, and current velocity, while lowest values could be registered for electric conductivity, water depth, and biological oxygen

demand after 5 days (BOD_5). Due to higher flexibility of the GAM approach, respective D values derived from this model range from 36 to 63.

Positions of the curve maxima (x_{max}) are listed in table 2. They indicate the values of the studied environmental parameters, at which the highest probabilities of occurrence for *Bythinella austriaca* may be expected. As depicted in figures 2 and 3, the maximum probability p_{max} generally ranges from 0.40 to 0.60, with highest values for water temperature, pH, and BOD_5 . With the GAM procedure, p_{max} of all variables is uniformly shifted to higher values (0.7 – 0.8). For all logistic model curves generated in this study, optimum ranges of $p(x)$ (r_{opt}) were uniformly defined by the parameters u and t . Within these intervals, the quotient of $p(x)$ and p_{max} does usually not fall below a value of 0.75 (i.e., the probability is equal as or greater than 75 % of the maximum probability of occurrence). In figures 2 and 3, optimum ranges are demarcated by the turning points ($p''(x) = 0$) at the limbs of the symmetrical probability curves. Widest intervals with respect to the overall ranges of the parameters were recorded for total hardness, current velocity, BOD_5 , and altitude, while narrowest ranges were obtained for temperature, pH, dissolved oxygen, and water depth (Tab. 2). The range of occurrence (r_{occ}) represents the interval, within which *Bythinella austriaca* can be found with a probability greater than 0.01. Due to the symmetrical shape of most regression curves, widest intervals of r_{occ} could be again recognized for total hardness, current velocity, BOD_5 and altitude, whereas narrowest r_{occ} was available for temperature, pH, dissolved oxygen, and water depth (Tab. 2). Where the lower limits of the modelled ranges fell below zero, they have been automatically assumed to take this value.

Discussion and Conclusions

As demonstrated in the results section, all environmental variables considered in this study have a significant influence on the distribution of *Bythinella austriaca*. Independent of the used model, the relationship between the probability of occurrence $p(x)$ and the environmental factor of interest could be uniformly expressed by bell-shaped regression curves. Computation of parameters necessary for an appropriate habitat characterization were so far limited to the logistic approach due to an extensive documentation in the open literature (e.g. PEETERS & GARDENIERS 1998).

Concerning the dependence of $p(x)$ on water temperature, *Bythinella* behaves as a stenotherm organism, whose optimum temperature range r_{opt} only covers a small interval (8.30 to 12.90 °C, Tab. 2). The model data correspond very well with previous observations on the spring snail (e.g. GLÖER & MEIER-BROOK 2003, TURNER et al. 1998, STURM 2000), where a preference of the gastropod for small isolated spring brooks with low water temperature could be found frequently. Similar to the small range of optimum temperatures, the occurrence of *Bythinella* is also limited to narrow pH intervals. As demonstrated in Fig. 2 and Tab. 2, for this specific variable r_{opt} ranges from 7.2 to 8.0, indicating neutral to slightly alkalic conditions. The spring snail, on the other hand, nearly disappears, where the pH-value declines below 6.0 and, thus, may be regarded as a highly acid-sensitive organism. These results are in a good correspondence with the largely accepted characterization of *Bythinella* as a main indicator for clear and unpolluted running waters (water category I; e.g. PATZNER 1994, BAUR 1998). Due to very low concentrations of acidic components (e.g. nitrates, see below), the pH usually varies between 7 and 8 in such waters. Acid-sensitivity of a similar extent was also reported for several gammarid species, with optimum pH-values ranging from about 7.5 to about 8.8 (SCHRIMPF & FOECKLER 1985, PEETERS & GARDENIERS 1998). As outlined in detail by BAUR (1998), pH tolerance may fluctuate significantly among freshwater organisms. Above all numerous fish species (e.g. trouts) were able to adapt to variable pH conditions over a long period of time, therefore tolerating both highly acidic and alkalic waters. Invertebrates usually do not follow this development, resulting in a limitation of their occurrence within smaller pH ranges. Essential parameters for an appropriate characterization of the water quality are,

besides the pH-value, the oxygen content and the biological oxygen demand after 5 days (BOD_5 , BAUR 1998). For water category I, the content of dissolved oxygen has to exceed 8 mg/L, whereas the BOD_5 should not be higher than 1 mg/L. Regarding the oxygen concentration, *Bythinella* prefers a range from 9.4 to 11.9 mg/L and tolerates a range from 7.0 to 14.3 mg/L (Tab. 2), underlining its reliability as an indicator organism for unpolluted waters. A slightly different result can be registered for the BOD_5 , where the upper limits of r_{opt} and r_{occ} fall into water category II with a BOD_5 range from 2 to 6 mg/L (BAUR 1998). In this specific case, the sensitivity of *Bythinella* seems to be lower than for the environmental parameters discussed above. This fact is also confirmed by the field data plotted into the respective graph of Fig. 3. Another physico-chemical factor strongly correlating with water quality and thus determining the distribution of the studied spring snail is the concentration of nitrate NO_3^- . In general, this component has to be regarded as the final product of the ammonium oxidation by diverse microorganisms. Nitrate is not categorized in the same way as oxygen content and BOD_5 for the classification of water quality, but the upper limit of NO_3^- in drink water is 50 mg/L, whereas rain water often contains 7 to 22 mg/L of the chemical compound (BAUR 1998). For *Bythinella*, the range of tolerated nitrate concentrations falls significantly below these two characteristic values. According to the presented data, occurrence of the gastropod is limited to $NO_3^- < 6$ mg/L, which, in most cases, is only realized in waters without any anthropogenic supply of nitrogen (GLÖER & MEIER-BROOK 2003, TURNER et al. 1998).

Ecological studies on *Bythinella* could uniformly demonstrate that the gastropod has a high dependence on the content of $CaCO_3$ in the water, which is the main constituent controlling conductivity and hardness (GLÖER & MEIER-BROOK 2003). The significance of this dependence is underlined by the distribution of the spring snail in the alpine region, where the transition zone between Northern Limestone and Central Alps corresponds with a complete disappearance of the species (e.g. STURM 1998, STURM 2000).

Besides the environmental parameters discussed above, occurrence of *Bythinella* additionally seems to show a meaningful dependence on water depth, altitude of the sample locality, and current velocity of the colonized waters (Fig. 3, Tab. 2). However, calculated values for maximum probabilities of occurrence and optimum ranges cannot be evaluated appropriately at the moment due to a lack of relevant literature data.

Since most recent modelling studies generally use non-parametric approaches for the investigation of similar relationships as those provided in the present work, simulation of $p(x)$ was additionally carried with the GAM procedure. As illustrated in figures 2 and 3, the GAM approach also produces bell-shaped regression curves which are characterized by 1) higher maxima of $p(x)$ and 2) a partly significant asymmetry, reflecting the distribution of data in a better way. However, most data points of the field investigation plot within the area demarcated by the parametric and non-parametric regression curves which may underline the importance of both models for a reliable prediction of species occurrence.

The present study has shown that for specific macroinvertebrates optimum ranges of diverse environmental variables can be derived successfully from large sets of respective ecological data by the application of parametric and non-parametric regression concepts. As a main result of the model approaches, a mathematical correlation between the probability of occurrence of a selected organism and an environmental variable may be described by well-defined functions. The importance of a variable for documenting the distribution of a macroinvertebrate is, on the one hand, reflected by the maximum probability p_{max} offered by the regression curve and, on the other hand, by the reduction in deviance D , representing the goodness-of-fit of the used ecological data (PEETERS & GARDENIERS 1998). The data of table 2 underline that all variables described in this study seem to have a similar significance for the characterization of habitats colonized by *Bythinella austriaca*. This can be regarded as rather plausible, as several parameters are marked by an interdependence (e.g. oxygen content, BOD_5 , and nitrate concentration; BAUR 1998). Due to the promising results of the study presented here, logistic regression and GAM have to be regarded as appropriate tools for a reconstruction of habitat requirements of aquatic molluscs and thus might find a further application in malacological sciences in the future.

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