Hydrobiologia **422/423:** 143–152, 2000.
M. Jungwirth, S. Muhar & S. Schmutz (eds), Assessing the Ecological Integrity of Running Waters.

The influence of environmental variables on the abundance of aquatic insects: a comparison of ordination and artificial neural networks

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Key words: artificial neural networks, ordination, aquatic insect emergence, prediction, discharge pattern

Abstract

Two methods to predict the abundance of the mayflies *Baetis rhodani* and *Baetis vernus* (Insecta, Ephemeroptera) in the Breitenbach (Central Germany), based on a long-term data set of species and environmental variables were compared. Statistic methods and canonical correspondence analysis (CCA) attributed abundance of emerged insects to a specific discharge pattern during their larval development. However, prediction (specimens per year) is limited to magnitudes of thousands of specimens (which is outside 25% of the mean). The application of artificial neural networks (ANN) with various methods of variable pre-selection increased the precision of the prediction. Although more than one appropriate pre-processing method or artificial neural networks was found, R^2 for the best abundance prediction was 0.62 for *B. rhodani* and 0.71 for *B. vernus*.

Introduction

Biodiversity, species richness, density or biomass of populations are results of a multitude of environmental variables. The dependence of a species or a community on its habitat is a crucial hypothesis in ecology. Thus, the forecast of abundance or biomass of species or populations, or even the community structure based on habitat characteristics is an interesting task in basic and applied ecology (Baran et al., 1996; Chon, 1996; Chon et al., 1996, Cisneros Mata et al., 1996; Whitehead et al., 1997). Such studies are of high interest in particular for managers of fish and wildlife, and for engineers dealing with stream and river channels (Giske et al., 1998; Guegan et al., 1998; Lek & Baran, 1997; Lek et al., 1996a; Mastorillo et al., 1997a; Mastorillo et al., 1997b).

During the past decades human-caused effects have altered the interactions between running waters and their environment, with implications on major portions of the community. A proper evaluation of human impact on ecosystems, however, depends on the availability of data from undisturbed reference areas. Intact systems need not only to be characterised in terms of average species abundance or the mean of selected environmental factors, but also in natural variability and its effects on populations and communities. This requires the availability of long-term data sets to generate models of the magnitude of the dependence of populations or communities on environmental variables. The results of such studies can generate features to characterise the ecological integrity of ecosystems. Regression and correlation models have repeatedly been used to explain patterns of ecosystem attributes and they have provided useful insights on environmental control of ecosystems, but their predictive power is low (Paruelo & Tomasel, 1997; Ter Braak & Verdonschot, 1995; Walley & Fontama, 1998).

Since 1969, the Limnologische Flußstation Schlitz (Germany) has collected data on emerging insects at the Breitenbach and on environmental variables that are believed to influence species abundance. Using traditional statistical methods and canonical correspondence analysis (CCA) (Ter Braak, 1988, 1990), the abundance of adults of individual species was attributed mainly to discharge patterns during larval development (Wagner & Schmidt, in press); this indicates that if the discharge pattern is known, at least the magnitude of a species' abundance (emerging adults) is predictable. Due to the necessity to recognise patterns and not just single events, artificial neuronal networks (ANN) are believed to be an alternative method to model species abundance (Colasanti, 1991; Lek et al., 1996b). The applicability of ANNs to this set of problems is tested below.

Study site

The Breitenbach is a small perennial stream in Central Germany, (50° 40′ N, 9° 45′ E) in an area of Bunter Sandstone. The stream flows mainly through meadows and has a drainage of approximately 9 km^2. The main spring in the middle course has an elevation of 310 m a.s.l., the stream flows into the Fulda River at 220 m a.s.l., and stream length is 2 km. Monitoring of insect emergence, water temperature and discharge was carried out at the 'classical site', 660 m below the spring (Illies, 1971), precipitation was measured at about 2 km distance from the drainage area, at an official site.

Material and methods

Species and environmental variables

Aquatic insects have been collected in emergence traps since 1969 (Illies, 1971). Collecting methods have changed: until 1986, insects were collected daily with a vacuum device, but in 1987 the traps were altered to collect specimens automatically. The mayflies *Baetis vernus* (Curtis, 1834) and*Baetis rhodani* (Pictet, 1843) are among the most numerous aquatic insects in the Breitenbach. Larvae of both species are grazers on stones and avoid sandy substratum (Wagner, 1989). *B. rhodani* is typically bivoltine, but *B. vernus* is univoltine with an egg diapause until winter (Bohle, 1969; Clifford, 1982; Schmidt, 1984). Mortality during the terrestrial phase of the life cycle was estimated to be 90–99% (Wernecke & Zwick, 1992). We compared the accuracy for predicting the abundance (A) of adult *B. vernus* and *B. rhodani* in the Breitenbach at one monitoring site with two methods described below. Water temperature (T) and discharge (D) were measured at the Breitenbach, and precipitation (P) was measured at a station close to the catchment. Monthly maxima of water temperature and discharge, and the monthly amount of precipitation, were used as predictors in the models.

Statistical methods

Correlation, regression (SPSS, 1997), and ordination (Ter Braak, 1988, 1990) are traditional methods to relate environmental variables with species abundance. They calculate abundance difference and provide methods to test significance. However, they involve data reduction to a smaller number of vectors or site points, with a loss of information.

As an alternative, artificial neural networks (ANN) use all available data of precipitation (P), discharge (D), water temperature (T), and abundance (A) of the 12 preceding months to predict species abundance in the target month (12 in Table 1).

ANNs consist of interconnected layers of simple processing elements called neurons. In feed forward networks — the most common type of ANNs — an input vector provided at the first layer (the input layer) is propagated step by step through all layers, resulting in an output vector at the last layer (output layer). If the neurons use a non-linear function to map their input (a weighted sum of all outputs from neurons in the previous layer) the network as a whole represents a non-linear function. The more neurons an ANN has, the more capable and complex the networks and its function becomes.

One of the most useful features of ANNs is the ability to learn relationships from examples, i.e., to adapt their weighted connections so that the network represents a model fitting the training data (usually a set of pairs of input vectors and corresponding target outputs). The rules for the adaptation process are put together in the learning algorithm. Given representative examples during training, ANNs also have the ability to generalise, i.e., provide sensible outputs for new (untrained) input vectors. The available data are split into a set of input/target pairs; these are used for the training and as a test set solely to check the generalisation performance of the trained net. This involves applying the input vectors and comparing the network's output with the target output. From that, an overall error value E is calculated by

$$E = \frac{1}{2\mathrm{PAT}} \sum_{p=0}^{\mathrm{PAT}-1} \sum_{i=0}^{\mathrm{OUT}-1} (\mathrm{tar}_{pi} - \mathrm{out}_{pi})^2,$$

where PAT is the number of patterns, OUT the number of output neurons, out_{pi} the value of the i-th output neuron for the p-th pattern, and tar_{pi} the target value of the i-th output neuron for the p-th pattern. For the experiments, we also calculated the determina-

Table 1. Structure of the 52-dimensional variable vectors. Abundance 12 is the target vector to be predicted by the remaining variable vectors

Variable	Index (13 subsequent months)												
Abundance	0	1	2	3	4	5	6	7	8	9	10	11	12
Discharge	0	1	2	3	4	5	6	7	8	9	10	11	12
Precipitation	0	1	2	3	4	5	6	7	8	9	10	11	12
Water temperature	0	1	2	3	4	5	6	7	8	9	10	11	12

Table 2. Number (rank on the *x*-axis in Figures 2, 4, 5, 6, 7) and date (year/month) of the test data set (7008 = 1970 August)

Date	No.	Date	No.	Date	No.	Date	No.	Date	No.
7008	1	7503	12	7910	23	8405	34	8812	45
7101	2	7508	13	8003	24	8410	35	8905	46
7106	3	7601	14	8008	25	8503	36	8910	47
7111	4	7606	15	8101	26	8508	37	9003	48
7204	5	7611	16	8106	27	8601	38	9008	49
7209	6	7704	17	8111	28	8606	39	9101	50
7302	7	7709	18	8204	29	8611	40	9106	51
7307	8	7802	19	8209	30	8704	41	9111	52
7312	9	7807	20	8302	31	8709	42	9204	53
7405	10	7812	21	8307	32	8802	43	9209	54
7410	11	7905	22	8312	33	8807	44		

tion coefficient R^2 for all output/target pairs in the test set. We used senso networks (Dapper, 1997), a simple but effective variation of feed-forward networks that implement the well-known back-propagation learning algorithm (Rumelhart et al., 1986). Senso nets contain an additional layer of weights, each corresponding to exactly one input neuron. These weights are included in the adaptation process (training) and provide a direct way to measure the relevance of the input variables in respect to the output variables. In addition, senso nets use some improvements of the standard back-propagation algorithm. We also carried out experiments with another kind of ANN called feature map (Kohonen, 1982).

Every model calculated is termed an experiment. Original data were scaled sigmoidally, exponentially, or logarithmically (minimum 0, maximum 1) to optimise the accuracy of the models. Furthermore, modelling with the entire database was compared with methods of a preceding reduction of vector dimensions by correlation, regression or neural sensitivity analysis (to reduce computing time). Eighty percent of the data sets were used in the training session; the remaining data were used as test data. A key for the year and months of the test data set is provided in Table 2.

Results

Ordination

The results of ordination (CCA) indicated a strong dependence of species abundance on the discharge pattern (Wagner & Schmidt, in press). Abundance (specimens per 5 m^{-2} $year^{-1}$) between patterns was significantly different (Figure 1). However, predictions can be made only in magnitudes of thousands of specimens per year.

Artificial neural networks (ANN)

Modelling the abundance of B. rhodani *(experiment 1)*

The precision of the model was relatively high (R^2=0.56) with the original data (April 1969 to December 1992). Almost all months with any abundance ($n > 0$) were predicted correctly. However,

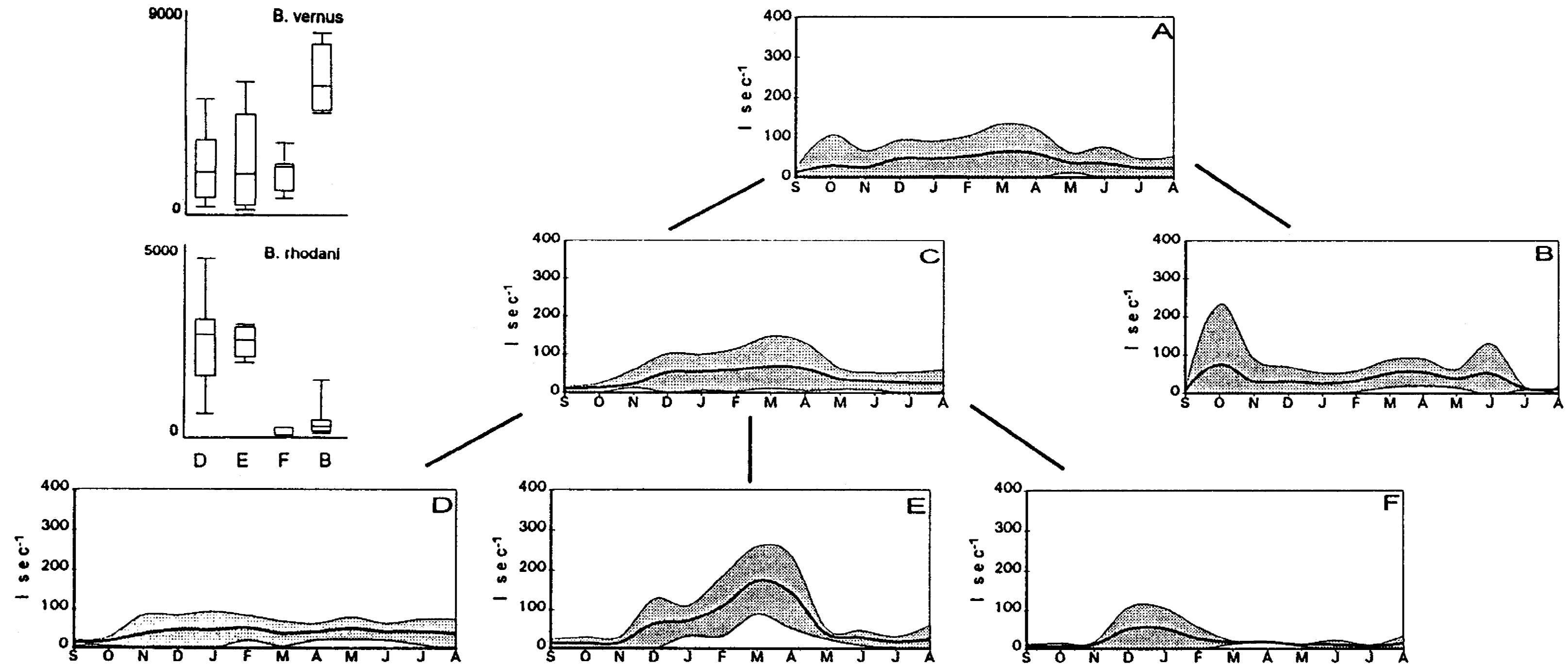

Figure 1. Discharge patterns of the Breitenbach discriminated with traditional statistical methods: (A) 25-year mean of monthly maximum discharge; (B) years with ‘non-seasonal’ events; (C) the seasonal pattern; (D) permanent, ‘good’ discharge; (E) winter and spring floods; (F) long-term low flow [mean of within group monthly maximum (line) ±1SD (stippled)]. The abundance of *B. vernus* and *B. rhodani* at patterns D, E, F and B, and significant differences between patterns ($P < 0.05$, Wilcoxon) on left top.

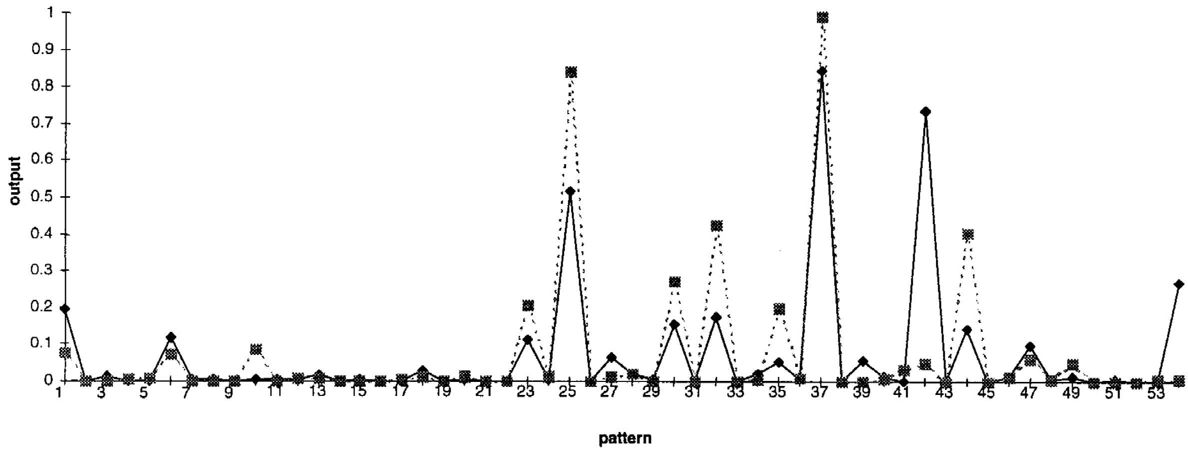

Figure 2. Abundance prediction of *B. rhodani*. Model: all input variables, best generalisation (lowest error): 51–10–1–senso net, R^2=0.56. (Model, full line, square; observed data, dotted line, quadrate).

Table 3. Overview of the different ANN models to predict the abundance of *B. rhodani*. Determination coefficient, minimum and mean generalisation errors of the models

Senso nets	Minimum	R^2	Mean
All variables	0.0082	0.56	0.0156
Correlation	0.0074	0.62	0.0108
Regression	0.0111	0.40	0.0151
Sensitivity analysis	0.0085	0.55	0.0139

Table 4. Overview of ANN models of *B. rhodani* abundance based on discharge measures. Determination coefficient, minimum, mean and maximum generalisation errors of the models

Method	Minimum	R^2	Mean	Maximum
Max	0.01600	0.11	0.02323	0.03453
Min	0.01853	0.18	0.02171	0.02993
MitMax	0.01423	0.37	0.01487	0.01556
Diff	0.01627	0.28	0.02305	0.03095
Quo	0.02166	0.01	0.02190	0.02256
Minus	0.02117	0.03	0.02649	0.03696
Div	0.02221	0.03	0.02850	0.03955

the magnitude of abundance differed between prediction and actual data (Figure 2). Pre-selection of five variables (abundance$_0$, abundance$_1$, abundance$_{11}$, temperature$_0$, temperature$_5$, compare Table 1) with correlation analysis increased the accuracy of the model to R^2=0.62 (Figures 3 and 4). Cross correlation indicated almost no influence of precipitation on *B. rhodani* abundance, but some influence of temperature and discharge. The abundance of the grandparent generation, low discharge and high temperature 12 months before, and high discharge with low temperature 6–8 months before emergence provide sufficient conditions for the success of the population. Pre-selection by regression analysis found other relevant variables (abundance$_1$, abundance$_{10}$, abundance$_{11}$, discharge$_6$, precipitation$_9$), yet decreased the accuracy of the model to R^2=0.40. A sensitivity analysis selected the variables abundance$_0$, abundance$_{11}$, discharge$_9$, precipitation$_9$, precipitation$_{10}$ and had an accuracy of R^2=0.55 (Figure 5). An overview of these experiments indicates that the best model was computed with a pre-selection of the 'best five' variables by correlation, and the next best models included all variables or a pre-selection by sensitivity analysis. A pre-selection by regression resulted in a low accuracy of the model (Table 3).

Altering the discharge data (experiment 2)

We also tested the prediction quality of the *B. rhodani* model using various measures of discharge only: maximum monthly discharge (Max), minimum monthly discharge (Min), the long-term mean pattern of monthly discharge (MitMax), the deviation of actual from long-term mean monthly discharge (Diff = Max minus MitMax), the quotient (Quo = Max by MitMax), difference of Max and Min (= Minus), and Div (= Max by Min). The highest R^2 of 0.37 was

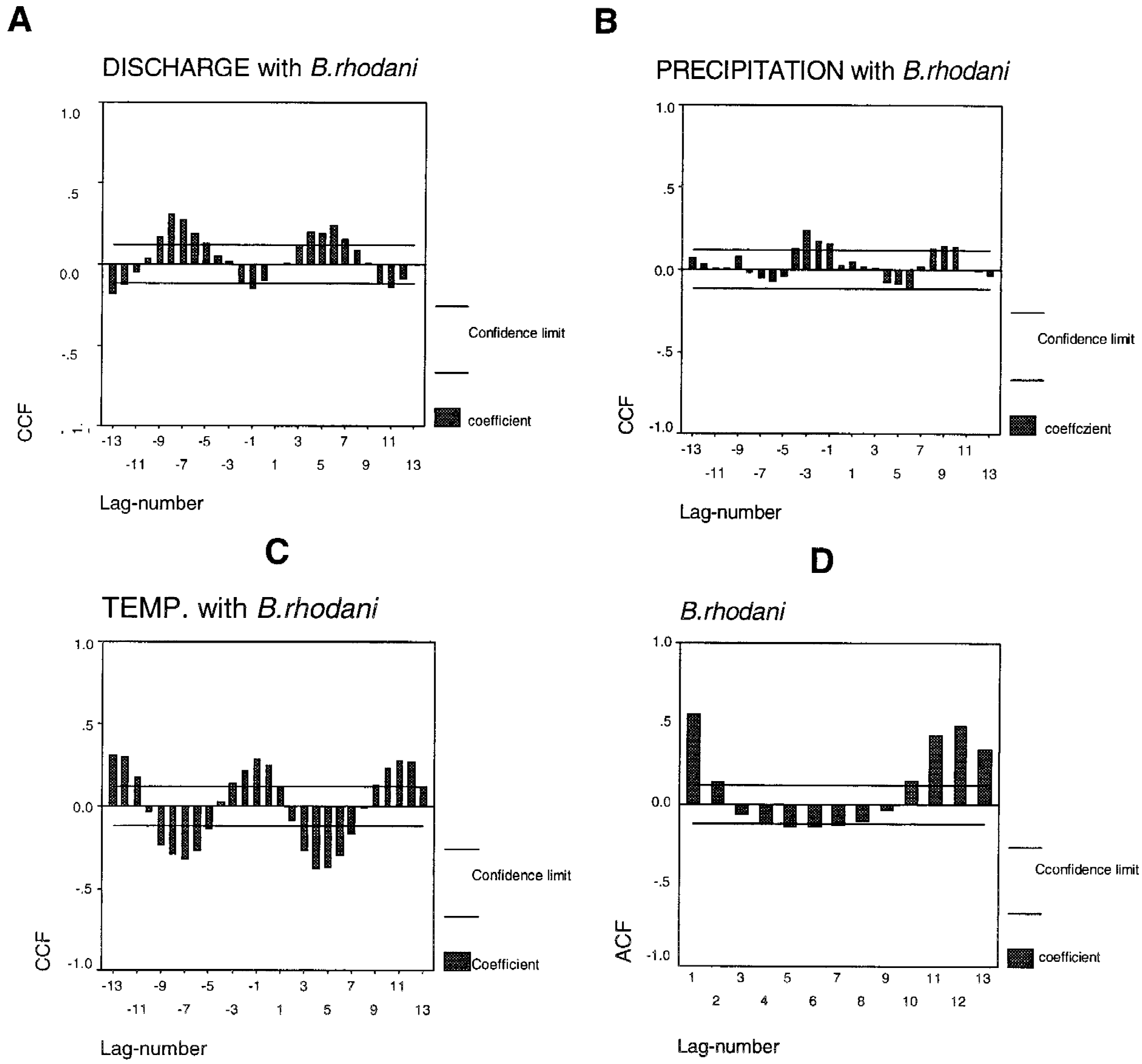

Figure 3. Auto- (ACF) and cross-correlation (CCF) of *B. rhodani* and environmental variables.

found with the long-term mean monthly discharge pattern, but the determination coefficient declined with discharge (Table 4).

Actual discharge or long-term mean discharge (experiment 3)

In a further experiment the actual discharge data (Max) of experiment 1 were replaced by the long-term mean discharge (MitMax of experiment 2) in combination with *P*, *T* and *A* to predict the abundance of *B. rhodani*. The determination coefficient increased to 0.63 for the model with all variables, but decreased to 0.57 for the correlation model.

Altering the scaling options (experiment 4)

The scaling options of the original data may contribute to variation of a model's precision. Thus, in experiment 4 the data were scaled logarithmically, exponentially, or sigmoidally. Variable pre-selection by correlation showed the best generalisation, although, after re-scaling the determination coefficient of the models decreased to 0.40–0.42 (Table 5).

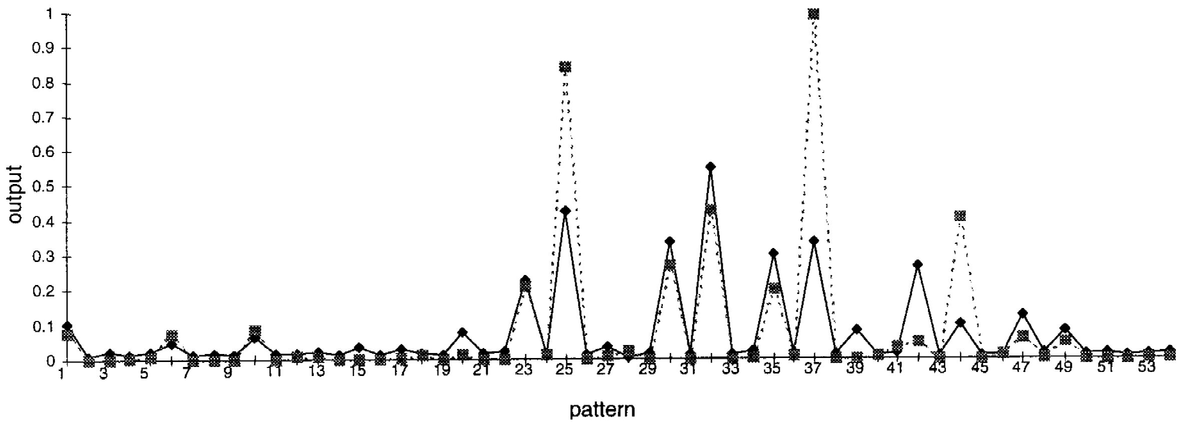

Figure 4. Abundance prediction of *B. rhodani*. Model: pre-selection by correlation, best generalisation (lowest error): 5–3–1–senso net, R^2=0.56. (Model, full line, square; observed data, dotted line, quadrate).

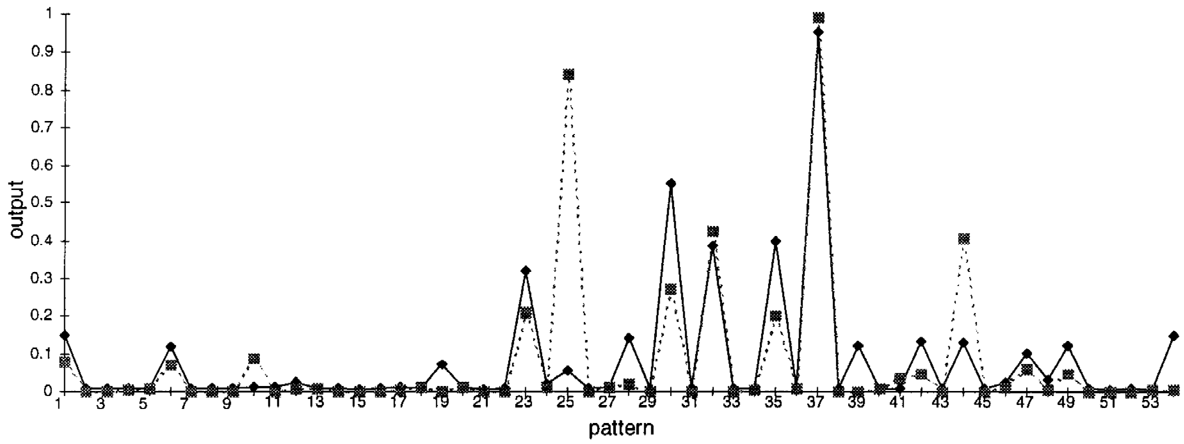

Figure 5. Abundance prediction of *B. rhodani*. Model: pre-selection by sensitivity analysis, best generalisation (lowest error) 5–3–1–senso net: R^2=0.55. (Model, full line, square; observed data, dotted line, quadrate).

Table 5. Overview of the ANN models with logarithmically scaled data. Minimum and mean generalisation errors of the models, and determination coefficient of the scaled and re-scaled data

Senso nets	Minimum	R^2	Mean	R^2 (re-scaled)
All variables	0.015	0.63	0.0164	0.40
Correlation	0.013	0.68	0.0147	0.42
Regression	0.016	0.59	0.0173	0.42

Table 6. Overview of ANN models of *B. vernus* abundance based on various pre-selection methods. Determination coefficient, minimum and mean generalisation errors of the models

Senso nets	Minimum	R^2	Mean
All variables	0.0057	0.54	0.0110
Correlation	0.0060	0.45	0.0087
Regression	0.0054	0.63	0.0077
Sensitivity analysis	0.0036	0.71	0.0064

Deviation of the actual data from the long-term mean (experiment 5)

We also tested the influence of the differences of the actual abundance and discharge values from the long-term mean. The model was not significant (R^2=0.01) with actual discharge and abundance, but with actual discharge and abundance of the parent generation the R^2 increased to 0.44.

Modelling the abundance of B. vernus *(experiment 6)*

The same models used for *B. rhodani* were applied to predict the abundance of *B. vernus*. A

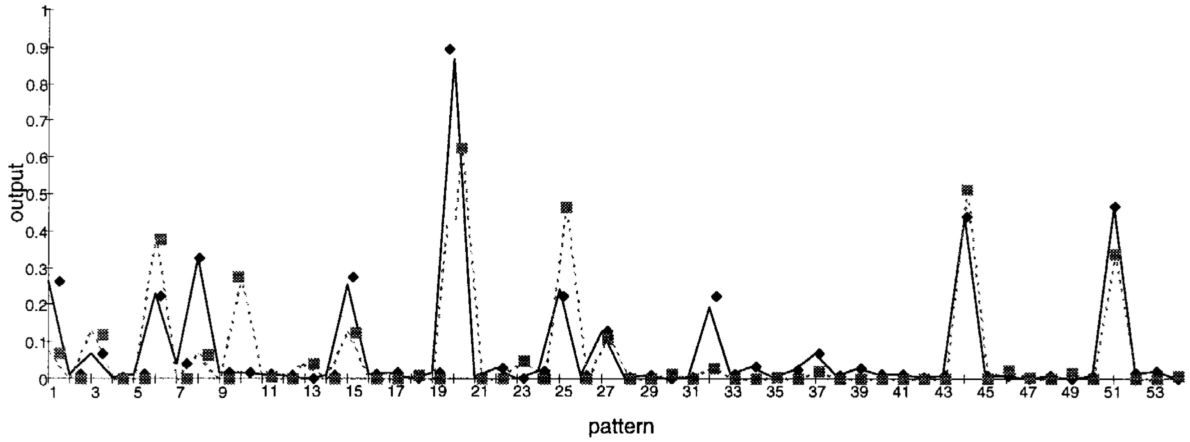

Figure 6. Abundance prediction of *B. vernus*. Model: pre-selection by sensitivity analysis, best generalisation (lowest error) 5–3–1–senso net: R^2=0.71. (Model, full line, square; observed data, dotted line, quadrate).

neural sensitivity analysis that selected the variables abundance$_0$, abundance$_{10}$, abundance$_{11}$, discharge$_0$, and precipitation$_0$ provided the best solution. The best model (5–3–1–senso net) had an accuracy of R^2=0.71 (Figure 6). The determination coefficient of other methods was lower, and lowest with pre-selection by correlation. An overview of the coefficient of other models for *B. vernus* is provided in Table 6.

Using only the months of larval development (experiment 7)

It was interesting to test whether the precision of the model increased if only months relevant for larval development (i.e., excluding the period of egg diapause until January) were used with the *B. vernus* data. We used previous abundance, discharge, precipitation and temperature data from six consecutive months to forecast the abundance in the last month by a 23–5–1 network. The resulting coefficient of this model was lower (R^2=0.60) compared with the regression model or the sensitivity analysis, but higher compared with a model that used all variables for an entire year.

Discussion and conclusion

The abundance differences of *B. rhodani* and *B. vernus* among years were related to discharge patterns using CCA and traditional statistics. However, only two classes with high and two classes with low abundance were discriminated for *B. rhodani*, whereas three classes of low and one class of high abundance were discriminated for *B. vernus*. Further discrimination was senseless because the 50% boxes of mean abundance per pattern widely overlapped (Figure 1). In combination with species traits, it can be deduced that *B. rhodani* has high success at permanently high discharge and at a seasonal discharge pattern (D, E), but low success at permanent low flow or a non-seasonal discharge pattern (F, B). *B. vernus*, on the other hand, reaches highest abundance values only at the non-seasonal pattern B. This is an example of discharge-mediated competitive exclusion because all probable competitors reach only low abundance levels as an effect of high discharge, but the *B. vernus* population remains more or less unaffected because of diapausing eggs.

ANN models are based on monthly data of species and environmental variables. The amount of data is larger in the original data set and computing is time consuming. The dimension reduction techniques provided improved generalisation performance of the ANNs in many, but not all cases. The selection of proper pre-processing methods is important for the success of the neural modelling (Dapper, 1997).

No single pre-processing method to model the abundance of both *Baetis* species was found. Pre-selection by correlation was optimal in *B. rhodani* but was the least sensitive method in *B. vernus*. *B. vernus* was best modelled by sensitivity pre-selection. Predictors for the best model of both species were abundance of the grandparent or parent generation and temperatures during the emergence and oviposition period of the grandparents and parents. Thus, abundance predictions can be made quite precisely even several months before emergence.

In both species, the manipulation of some or all data by different scaling options decreased the precision of the ANN models (comparison of R^2 values is useful only after re-scaling). A similar phenomenon was observed in CCA analyses (Wagner & Schmidt, in press). Several combinations of long-term and actual data also did not improve the model. Only one small but negligible improvement was observed in the *B. rhodani* model, if the actual discharge was replaced by the long-term mean, but the previously best (correlation) model then decreased in precision. Ecologically, a probable link of the species' life cycle with repetitive seasonal patterns of the environmental variables exists and probably it explains the high determination coefficients of the ANN models.

Based also on the results of more traditional statistical methods, increased experience with ANNs will help optimise the models to predict the abundance of aquatic insects. These methods can be further developed as a tool for better understanding the interrelations of environmental variables impacting individual species and the entire community of streams. The forecast of environmental effects on habitats, species, populations and communities is crucial in basic as well as in applied science.

Acknowledgements

This study was supported by a grant of the Deutsche Forschungsgemeinschaft 'Modellierung ökosystemarer Zusammenhänge in Fließgewässern mit Neuronalen Netzen' (BO 1012). We thank the numerous people who have contributed for many years in the collection of the data. In recent years E. Döring, G. Stüber, and B. Landvogt-Piesche contributed most to these data sets. They, like many assistants and students, were involved in this study by collecting and determining emerged insects, or by recording environmental variables. T. Horvath provided linguistic help. We sincerely acknowledge the comments of two anonymous reviewers on the manuscript.

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