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PRIMARY RESEARCH PAPER

# Which factors affect phytoplankton biomass in shallow eutrophic lakes?

**Gábor Borics · Levente Nagy · Stefan Miron · István Grigorszky · Zsolt László-Nagy · Balázs A. Lukács · László G-Tóth · Gábor Várbíró**

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**Abstract** The restoration and management of shallow, pond-like systems are hindered by limitations in the applicability of the well-known models describing the relationship between nutrients and lake phytoplankton biomass in higher ranges of nutrient concentration. Trophic models for naturally eutrophic small, shallow, endorheic lakes have not yet been developed, even though these are the most frequent standing waters in continental lowlands. The aim of this study was to identify variables that can be considered as main drivers of phytoplankton biomass and to build a predictive model. The influence of potential drivers of phytoplankton biomass (nutrients, other chemical variables, land use, lake use and lake depth) from 24 shallow eutrophic lakes was tested using data in the Pannonian ecoregion (Hungary and Romania). By incorporating lake depth, TP, TN and lake use as independent and Chl-*a* as dependent variables into different models (multiple regression model, GLM and multilayer perception model) predictive models were built. These models explained >50% of the variance. Although phytoplankton biomass in small, shallow, enriched lakes is strongly influenced by stochastic effects, our results suggest that phytoplankton biomass can be predicted by applying a multiple stressor approach, and that the model results can be used for management purposes.

**Keywords** Phytoplankton · Carpathian Basin · Lake use · Land use · Nutrients

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G. Borics · B. A. Lukács · L. G-Tóth · G. Várbíró (✉)
MTA Centre for Ecological Research, Department
of Tisza River Research, Bem sqr. 18/c,
Debrecen 4026, Hungary
e-mail: varbiro.gabor@okologia.mta.hu

L. Nagy
Romanian Water Authority, Somes-Tisa Branch, Str.
Vanatorului nr. 17, 400213 Cluj-Napoca, Romania

S. Miron
Romanian Water Authority, Prut-Barlad Branch,
Str. Th. Vascauteanu nr. 10, 700462 Iasi, Romania

I. Grigorszky
Department of Hydrobiology, Debrecen University,
Egyetem sqr. 1, Debrecen 4032, Hungary

Z. László-Nagy
Environmental Protection, Nature Conservation
and Water Authority, Lower-Tisza Region,
Felső Tisza-part 17, Szeged 6721, Hungary

## Introduction

Small, shallow lakes such as oxbows and fluvial ponds are characteristic types of standing waters in lowland areas. Lowlands are the most densely populated areas of the world, which often means high risks of degradation of standing waters. The frequently occurring noxious algal blooms and their severe consequences for the lakes' ecosystem services triggered the elaboration of lake management strategies. After the adoption of the Water Framework Directive (EC, 2000), all European Union member states are obliged to assess the ecological quality of waters and to elaborate management plans. The first step in lake management is generally the reduction of nutrient load. Due to an increasing public awareness of eutrophication and related problems, the study of the relationship between nutrients and lake trophic status has received widespread attention since the 1960s (Johnson & Vallentyne, 1971; Likens, 1972; Rast & Lee, 1978; Janus & Vollenveider, 1981, Carpenter & Capone, 1983). Several empirical models were built to describe the functional relationship between principal macronutrients (TN and TP) and phytoplankton biomass (Dillon & Rigler, 1974; Jones & Bachmann, 1976; Rast & Lee, 1978; Clasen & Bernhardt, 1980; OECD, 1982; Canfield, 1983; Havens & Nürnberg, 2004; Phillips et al., 2008). These models suggest linear relationships between the logarithmically transformed values of the annual mean or vegetation period mean TP and chlorophyll-*a* (Chl-*a*) concentration as a proxy of phytoplankton biomass. Nevertheless, the strength of this relationship depends on a range of variables. Several authors found (Canfield, 1983; Prairie et al., 1989) that the linear relationship is valid only for the lower ranges ($TP < 5–100\ \mu g\ l^{-1}$) of the TP concentration. At higher ranges ($TP > 100\ \mu g\ l^{-1}$), the relationship appears to be asymptotic. Similar findings were published by Phillips et al. (2008) who analysed a large European dataset and demonstrated that the $Chl\text{-}a = f(TP)$ relationship is not linear because the slope of the line fitted by a LOESS method in the $TP < 100\ \mu g\ l^{-1}$ range is larger than that in $TP > 100\ \mu g\ l^{-1}$ range. Similar results were found for the $Chl\text{-}a = f(TN)$ model, where the break point is at $TN = 1{,}700\ \mu g\ l^{-1}$. These observations raise the question that if TP is not a strong predictor of phytoplankton biomass in the higher concentration ranges, what factors influence the productivity of lakes in highly eutrophic conditions? Answering this question is particularly crucial for the management and restoration of very shallow ($Z_{mean} < 3$ m) lowland lakes such as steppe and prairie lakes. Due to natural variation in variables such as lake morphometry, climate, aquatic vegetation, basin geology or physical and chemical characteristics of lake water, shallow lakes constitute a highly variable lake type (Nõges et al., 2003; Borics et al., 2012). In continental climates, due to the high evaporation/precipitation ratio (Szesztay, 1960) and low geographic relief, these water bodies have long water residence times, are practically endorheic and naturally eutrophic (Allan et al., 1980). The nutrient content of these lakes (even in a natural state) is typically found at a concentration range where the $Chl\text{-}a = f(\text{nutrients})$ models show asymptotic behaviour and can be characterised by increased variation. Therefore, the applicability of these models for water management purposes is strongly limited for shallow lakes.

In this study, we investigate the factors that influence the phytoplankton biomass of shallow lakes either directly (macronutrients, pH, conductivity, water depth) or indirectly (land use, lake use) using data on Hungarian and Romanian lakes from national archives. Our aim was to identify the main drivers of algal biomass production and to demonstrate that phytoplankton biomass can be adequately predicted by linear and nonlinear models in such systems.

## Materials and methods

### Study area

The study was carried out in the Pannonian Lowland Ecoregion (Central Europe), which lies in the westernmost part of the Eurasian Steppe Zone and includes lowlands of the Carpathian Basin and alluvial plains of the Lower Danube River. The annual mean temperature of the region is about 10–12 °C (summer mean temperature is 21–23 °C) and the average annual precipitation is 450–600 mm. Most of the natural lakes in the area are oxbows created by meandering rivers and lakes developed in deflation pools. We investigated 24 water bodies (Table 1). Lakes were selected to include a high range of the various stressors considered in the study.

### Sampling and sample processing

Phytoplankton Chl-*a* data and background variables (pH, electrical conductivity, TP, TN) were provided by the national lake monitoring systems maintained by the Hungarian Ministry of Rural Development and by ‘Romanian Waters’ National Administration. Sampling and measurement of the biological and physical variables were harmonised between Hungary and Romania and the results were compared and checked

**Table 1** Morphological characteristics of the lakes investigated

| Lake name | Lake years | Type | Mean depth (m) | Area (ha) |
|---|---|---|---|---|
| Atkai Holt-Tisza | 1 | Oxbow | 3.2 | 107 |
| Egyek-Kócsi Tározó | 3 | Deflation pool | 2 | 3.5 |
| Morotvaközi Holt-Tisza | 3 | Oxbow | 1.4 | 87 |
| Snagov | 2 | Deflation pool | 3 | 575 |
| Szelidi-tó | 1 | Oxbow | 3 | 51 |
| Szöglegelői Holt-Tisza | 1 | Oxbow | 1.5 | 1.1 |
| Darab-Tisza | 5 | Oxbow | 1.5 | 8.4 |
| Falu-Tisza | 5 | Oxbow | 3.2 | 21.6 |
| Malom-Tisza 1 | 1 | Oxbow | 5 | 38.5 |
| Malom-Tisza 2 | 3 | Oxbow | 2.5 | 5.6 |
| Egyeki Holt-Tisza | 4 | Oxbow | 1.2 | 86 |
| Félhalmi Holt-Körös | 1 | Oxbow | 1.6 | 73 |
| Nagyréti-tó | 1 | Deflation pool | 1.75 | 211 |
| Szarvas-Békésszentandrási Holt-Körös | 2 | Oxbow | 1.8 | 206 |
| Galaţui | 1 | Deflation pool | 3 | 712 |
| Holt-Szamos, Géberjén | 2 | Oxbow | 1.3 | 100 |
| Holt-Szamos, Tunyogmatolcs | 2 | Oxbow | 3 | 85 |
| Rétközi-tó | 1 | Deflation pool | 1.3 | 427 |
| Felső-Darab-Tisza | 2 | Oxbow | 1 | 0.85 |
| Szűcs-Tisza | 5 | Oxbow | 2.5 | 8 |
| Fancsika 1 | 1 | Deflation pool | 1.2 | 82 |
| Fancsika 2 | 1 | Deflation pool | 1.2 | 43 |
| Kati-tó | 2 | Deflation pool | 1.7 | 12 |
| Mézeshegyi-tó | 3 | Deflation pool | 0.6 | 50 |

by annual intercomparison exercises. For the analysis of phytoplankton and background variables, monthly samples were taken from the photic layer (2.5 × Secchi depth) of lakes in the summer period (June–September). Data spanning this period were averaged, thus the lake-year was our observation unit. Altogether 53 lake-years data were involved in the analyses (Table 1). Phytoplankton biomass was approximated by sestonic Chl-*a* concentration, which was measured spectrophotometrically and corrected for phaeophytin (ISO 10260, 1992). Mean depths of lakes were calculated based on lake volume and surface data provided by the water authorities.

## Lake use

Recreational fishing/angling is the most important type of lake use in the region. Data on fishing activity and fish abundance were provided by the lake users and the regional water authorities.

To reduce errors from the uncertainty of fish abundance, the intensity of fishing was estimated at an ordinal scale as follows: (i) no fishing/angling activity and no artificial stocking of fish, fish abundance $<50$ kg ha$^{-1}$; (ii) moderate fishing/angling activity with occasional artificial fish stocking, fish abundance is between 50 and 200 kg ha$^{-1}$; and (iii) intensive fishing/angling, regular fish stocking, fish abundance $>200$ kg ha$^{-1}$.

## Land use

Several lakes in the lowlands of the continental region either do not have inlets or their water supply is occasional and is not substantial. Water loss is balanced primarily by precipitation and groundwater input, therefore, the delineation of the watershed is often problematic. Thus, we considered the area within 500 m from the shoreline in the calculation of the spatial distribution of land-use categories. Four land-use categories (urban, intensive agriculture, non-intensive agriculture, natural forests and natural wetlands) were expressed as percentage of total area. Land-use information was derived from the 1:50,000 scale CORINE database and from orthophotos of the areas (we must note that applying broader area results in very high ratio of intensive agriculture in case of all lakes, and this kind of 'homogenization' makes the analyses worthless).

### Statistical analyses

Physical and chemical variables were logarithmically transformed. Ordinary least-squares linear regression analyses were used to examine the relationship between the possible predictor variables and Chl-*a* as an approximate measure of phytoplankton biomass. One-way ANOVA was used to test differences in phytoplankton biomass among the three lake-use categories.

For modelling the effects of multiple factors on phytoplankton biomass, we applied three multivariate models: a multiple linear regression model (MRM), a general linear model (GLM) and an artificial neural network (ANN). The ANN approach has been developed and tested using multilayer perception (MLP) models, the goal of which is to minimise the mean square error between the predicted output concentrations of the network and the observed concentrations. The MLP consists of three layers. The first layer, called the input layer in our case, comprises four neurons corresponding to the four input parameters as log TN, log TP, log depth and lake use. The result layer, called the output layer, comprises a single neuron corresponding to the value of the predicted dependent variable (log Chl-*a* concentration). The layers between the input and output layers are called the hidden layers. In our model, the hidden layer consists of 12 neurons. The MLPs were trained using the Levenberg–Marquardt learning algorithm. The dataset were divided into 80% training and 20% for testing dataset.

GLM and ANN models were constructed in the Matlab environment (The MathWorks Inc., 2000).

## Results

The relationships between potential predictor variables and phytoplankton biomass (Chl-*a*) are presented graphically as scatter plots (Fig. 1). Correlation and regression coefficients, equations and the level of significance are shown in Table 2. We found a significant ($P < 0.05$) but weak relationship between TN and Chl-*a* (Table 2), while the TP–Chl-*a* relationship was not significant. In our data, phosphorus values were in the range where the TP–Chl-*a* relationship is apparently asymptotic. We note that the TP–Chl-*a* relationship was significant in the lower (TP $\sim$ 0–400 $\mu l^{-1}$) range ($P < 0.05$; $R^2 = 0.3009$). However, there were several lakes dominated by floating leaved macrophytes in the higher (>400 $\mu l^{-1}$) TP range and these were characterised by low phytoplankton biomass.

The weak but significant relationship between TN and phytoplankton biomass agrees well with previous findings (Nürnberg, 1996). Phillips et al. (2008) demonstrated that the TN–Chl-*a* relationship is linear up to TN $\sim$ 1,700 $\mu g\ l^{-1}$ concentration value; above this range, the relationship is asymptotic. However, for our dataset the increasing tendency of phytoplankton biomass could also be observed, but the regression line was characterised by low slope and $R^2$ value (Table 2).

Inorganic nitrogen forms show high within-year variation, therefore, it was not surprising that $NO_3$ ions showed no correlation with phytoplankton biomass. The reason is that inorganic forms of nitrogen are strongly involved in microbial processes in aquatic environment.

Contrary to nitrate ammonium concentration showed a significant positive relationship with phytoplankton biomass. The explained variance was high ($R^2 = 0.24$) but was due to some extremely large ($NH_4 > 200\ \mu g\ l^{-1}$) values. Considerable within-year variation of ammonium was observed in our dataset (not shown here), therefore, we reckon that high ammonium concentration cannot be reason for high algal biomass; rather, it is a consequence of it. The pH also showed strong and highly significant linear relationships with phytoplankton biomass with relatively high proportions of variance explained (Table 2). However, the pH was not included in the predictive models, because it cannot be considered an explanatory variable for Chl-*a*. The difference of one order of magnitude between the conductivity values of the lakes in our data was large enough to reveal its possible impact on phytoplankton biomass, however, such a relationship was not found. This is not surprising because there is no convincing reason to assume that in this range the concentration of

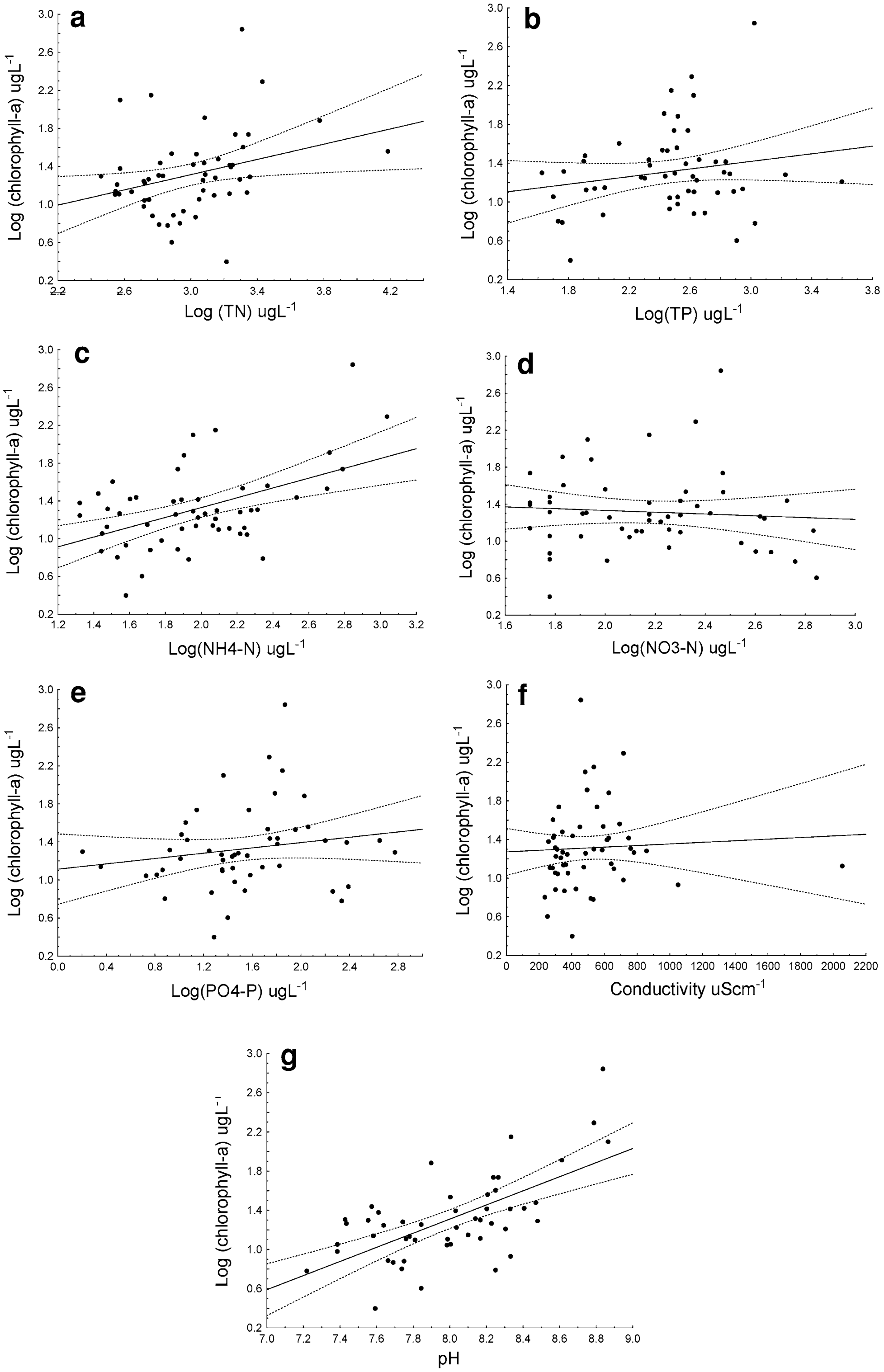

**Fig. 1** Scatterplots and linear regression lines for the relationships between predictor variables and Chl-*a*. *TP* total phosphorus, *TN* total nitrogen, *NO$_3$-N* nitrate nitrogen, *IP* inorganic phosphorus, *NH$_4$* ammonium nitrogen, *Z* depth. *Dotted lines* indicate 95% confidence intervals around regression lines

**Table 2** Regression equations for $\log_{10}$ Chl-*a* concentration as a function of potential descriptor variables

| Variables | Equation | *R* | *P* |
|---|---|---|---|
| Log depth | $1.5661 - 0.9694x$ | −0.4517 | 0.0007 |
| Log TP | $0.8306 + 0.196x$ | 0.1905 | 0.1718 |
| Log TN | $0.1125 + 0.4005x$ | 0.3076 | 0.0251 |
| Log COD | $0.9219 + 0.0084x$ | 0.6836 | 0.0000 |
| Log $NO_3$-N | $1.5249 - 0.0966x$ | −0.0745 | 0.5998 |
| Log $NH_4$-N | $0.2894 + 0.5198x$ | 0.4938 | 0.0002 |
| Log $PO_4$-P | $1.1136 + 0.1397x$ | 0.1745 | 0.2256 |
| Log pH | $-4.4526 + 0.7204x$ | 0.6466 | 0.0000 |
| Log electrical conductivity | $1.2709 + 0.00008x$ | 0.0548 | 0.0697 |
| Urban areas | $1.3461 - 0.0052x$ | −0.1143 | 0.4152 |
| Intensive agriculture | $1.4964 - 0.0031x$ | −0.2337 | 0.0921 |
| Non-intensive agriculture | $1.282 + 0.0055x$ | 0.1496 | 0.2851 |
| Forests and natural wetlands | $1.2358 + 0.0027x$ | 0.2093 | 0.1325 |

dissolved ions has any impact on the nutrient uptake or on the proliferation of algae.

Hydrobiological characteristics of shallow lakes are different from those of deep ones, therefore, lake morphometry should be taken into account when the trophic state of lakes is compared (Vollenweider, 1968). In the present study, we focused exclusively on shallow lakes (mean depth $< 3.5$ m), but our results suggested that lake depth might be an important attribute even in such lakes. The inverse relationship was highly significant, and compared to other potential descriptor variables (nutrients, land use) could be characterised by higher $R^2$ value.

Linear regression analysis demonstrated a lack of relationship between each of the land-use categories and phytoplankton biomass (Fig. 1). In contrast, one-way ANOVA revealed a highly significant ($F$[2;50]: 33.9021; $P < 0.05$) difference in Chl-*a* among the three lake-use categories (Fig. 2f).

For modelling the mutual effect of multiple factors, we selected variables that have a causal relationship with phytoplankton biomass based on our current knowledge. These were total phosphorous (TP), total nitrogen (TN), lake depth and lake use as a categorical predictor.

All three predictive models demonstrated that the selected variables had relevant roles in shaping phytoplankton biomass (Table 3). The multiple regression resulted in an adjusted $R^2$ value of 0.49 ($F$[4,48]: 13.67; $P < 0.0001$) (Fig. 3a). The GLM showed a stronger relationship, with an adjusted $R^2$ of 0.579 ($F$[5,47]: 15.30; $P < 0.0001$) (Fig. 3b). After ANN learning with the training set of data, we obtained an adjusted $R^2$ of 0.731 for the whole data set. The latter model appeared to have the best fit (Fig. 3c). MRM and GLM performed almost equally well, while ANN (MLP network) was found to perform slightly better. Conventional techniques such as multiple regression and GLM are widespread within ecology but have some shortcomings. These shortcomings arise from the facts that relationships between variables in environmental sciences are often nonlinear and that data rarely have normal errors. The ANN is a powerful computational technique for modelling complex relationships in situations where the proper form of the relation between the variables is unknown or nonlinear (Chen & Billings, 1992). Such nonlinear relationships may be present in our data as well (e.g. asymptotic TP–Chl-*a* relationship at high TP concentration), which may be the reason for the higher performance of the ANN compared to MRM and GLM.

## Discussion

Although the TP–Chl-*a* relationship was not significant over the entire concentration range we cannot say that TP has no impact on the phytoplankton biomass in shallow eutrophic systems. The maximum carrying capacity of phytoplankton biomass is related to the nutrient content even in the case of eutrophic lakes.

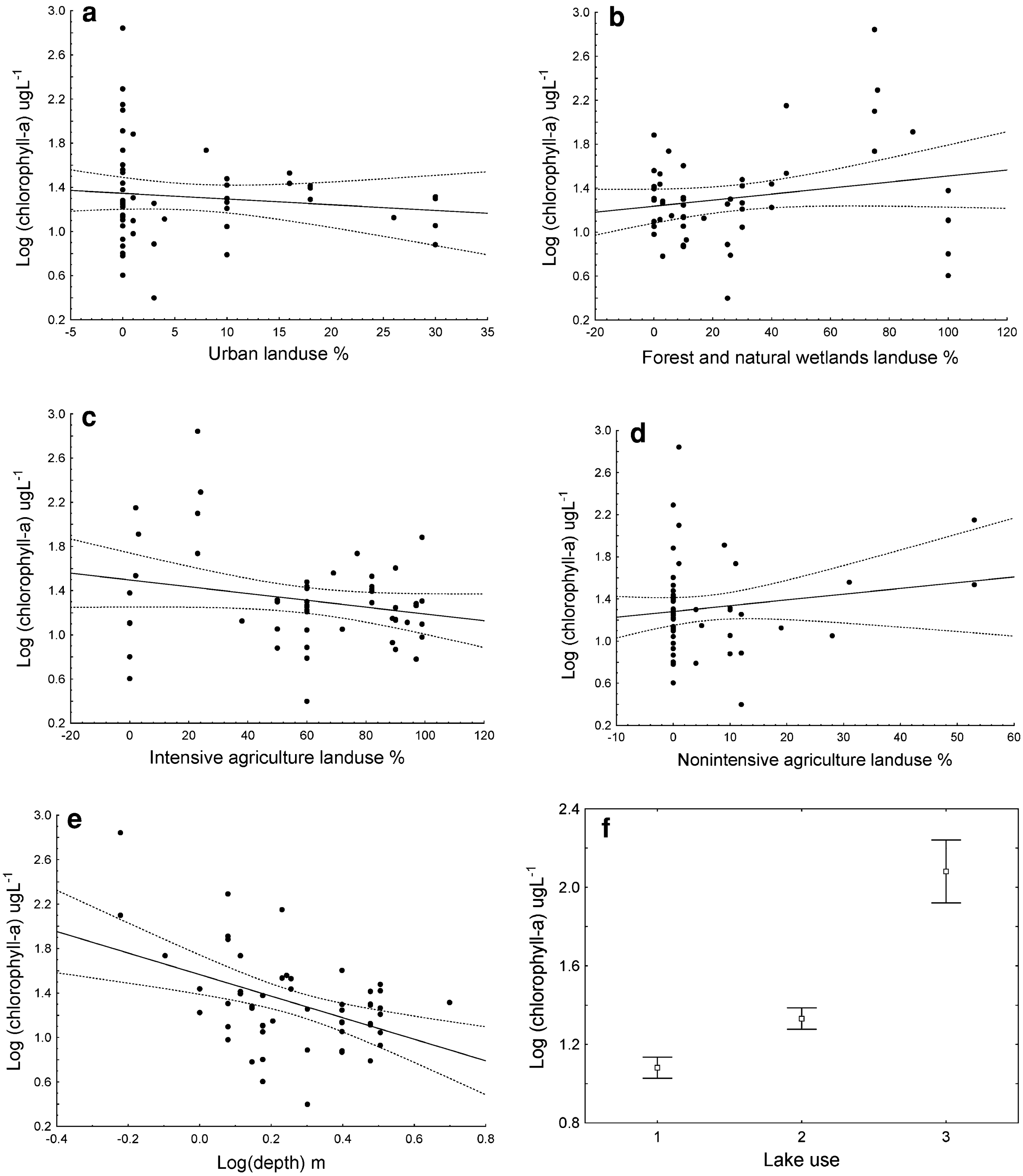

**Fig. 2** Scatterplots and linear regression lines for the land-use categories (**a**–**d**) and water depth (**e**) as descriptors, versus Chl-*a*. **f** Mean values and standard errors of Chl-*a* in the three lake-use categories. ANOVA ($F$[2;50]: 33.9021; $P < 0.05$)

Hyper-eutrophic lakes have higher maximum carrying capacity than eutrophic ones, and under favourable hydro-meteorological conditions this difference manifests in extremely high phytoplankton biomass (Borics et al., 2000). Therefore, slight increasing tendency in phytoplankton biomass can be expected

**Table 3** Regression equations, adjusted $R^2$ values and levels of significance for the three (GLM, MRM, ANN) models

| | Formula | Adjusted $R^2$ | $F$ | $P$ |
|---|---|---|---|---|
| GLM | Lakeuse = 1<br>LogChla = 0.030017537logdepth + 0.144491560 log TP + 0.374241789 log TN − 0.35551660<br>Lakeuse = 2<br>LogChla = 0.030017537logdepth + 0.144491560 log TP + 0.374241789 log TN − 0.35551660 − 0.20417145<br>Lakeuse = 3<br>LogChla = 0.030017537logdepth + 0.144491560 log TP + 0.374241789 log TN | 0.579 | 15.30 | 0.000 |
| Multiple regression | LogChla = −0.087180 log depth + 0.042447 logTP + 0.148944 logTN + 0.617997 lakeuse + 0.0507544068335727 | 0.493 | 13.67 | 0.000 |
| Neural networks | – | 0.731 | 180.36 | 0.000 |

even in the eutrophic–hypertrophic range. Ammonium showed the closest relationship with Chl-*a*. It is generally believed that ammonium utilisation, due to its favourable energy requirement (Ward & Wetzel, 1980; Syrett, 1981) is preferred by algae, therefore, it seems a plausible explanation for the $NH_4$–Chl-*a* relationship. However, we believe that this relationship is not causal. Parallel with the development of algal blooms, the mineralization of decaying algal cells is also enhanced. During decomposition of nitrogen-containing organic compounds, ammonium ions always occur in water even in well-oxygenated environments.

Regarding the physical characteristics of lake water only the pH showed significant relationship with phytoplankton biomass. Although at high pH the photosynthesis can be inhibited by the lack of available $CO_2$ this phenomenon was not observed in this study.

Our results demonstrated that lake depth is crucial in shaping phytoplankton biomass in shallow lakes. It is known that phytoplankton density is inversely proportional to mixing depth (Huisman, 1999), and, in very shallow polymictic lakes, implicitly, to the total depth of the lakes. The depth of the studied lakes ranged between 0.6 and 3.5 ms, and this high ($\sim 6\times$) difference appeared in the Chl-*a* values. We therefore think that lake depth cannot be set aside during modelling phytoplankton biomass in shallow lake ecosystems.

It has long been recognised that the ecological status of aquatic systems depends on the surrounding terrestrial environment (Cummins, 1974; Hynes, 1975). The high percentage of natural land use is one of the most important criteria to be considered in the selection of reference lakes in Europe (Poikāne et al., 2010). Surprisingly, our findings suggest that the type of land use is not an important driver of productivity of shallow lakes' phytoplankton.

The possible reasons of this contradiction include the special geomorphology and climate of the watersheds. In mountainous and hilly regions, the undesirable products of anthropogenic land use directly threaten the lakes and the tributary streams due to surface runoff (Omernik, 1976, Osborne & Wiley, 1988). In contrast, runoff is considerably less in flat lowlands, where land-use activities might have direct influence only on the nutrient content of the shallow ground water (Leone et al., 2009). Nevertheless, we must note that because of the arbitrary definition of catchment area statements about land-use effect are less reliable as compared with those of other descriptor variables.

Angling is the dominant form of lake use in the region. Stocking of fish (both benthivorous and planktivorous ones) has serious consequences for shallow lake ecosystems. Benthivorous species act as a nutrient pump from sediment to water column (Roberts et al., 1995), while planktivorous species (especially the frequently introduced invasive silver carp) can reduce the number of large zooplanktic grazers (Carpenter et al., 1985; Van de Bund & Van Donk, 2002). Moreover, fish food added by anglers means additional nutrient input to the lakes. This

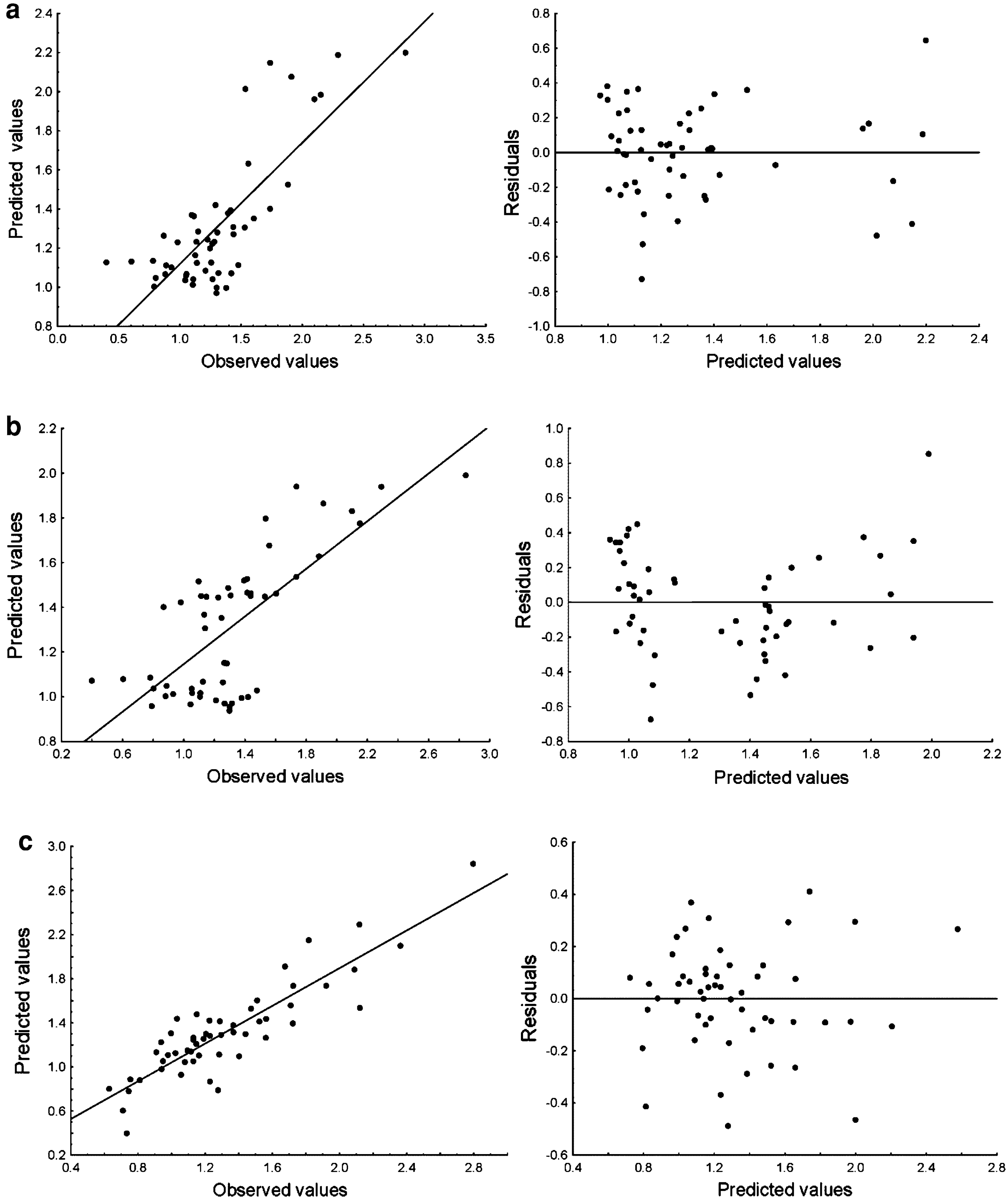

**Fig. 3** Scatterplots of the observed versus predicted $\log_{10}$ Chl-*a* values based on the three models and distribution of residuals. **a** GLM, **b** MRM and **c** ANN

activity means an intensive fertilisation of lakes and can be considered as the main source of external nutrient load. Artificial stocking of fish and the maintenance of huge fish stock drives these systems to a phytoplankton-dominated state where bottom-up control is the principal mechanism (Scheffer, 1998). The various levels of lake use had considerable impact on the macrophyte abundance of the lakes studied. Abundant and divers macrophyte coverage characterised the lakes where fishing was insignificant, while the most heavily fished lakes were devoid of both submerged and floating leaved macrophytes. These observations are in accordance with the experiences gained from the lake biomanipulation studies of the last decades (Shapiro et al., 1975; Carpenter et al., 1985; Benndorf, 1995; Meijer, 2000; Catalano et al., 2010), i.e. manipulation of fish population basically influences the lakes' food web structure, and results in macrophyte-dominated or turbid state. Investigating the trophic structure of eutrophic Danish lakes, Jeppesen et al. (2000) demonstrated that lake restoration by the manipulation of fish populations can be successful if the TP concentration does not exceed 100 μg $l^{-1}$. Contrary to this opinion, accidental fish kills (Borics et al., 2000) and lake experiments (Tátrai et al., 2009) demonstrated that manipulation of the fish results in a decrease in the Chl-*a* concentrations even in those cases where measures of nutrient removal were not taken. After fish removal invasion of macrophytes were observed in both cases but these events did not coincide with reduction of nutrients. High abundance of macrophytes and high concentration of nutrients can occur simultaneously, which is clearly indicated by the high variance of Chl-*a* data at the higher TP range (Fig. 1b). Although TP concentrations exceeded the desired 100 μg $l^{-1}$ value in our study, lake use appeared to be the best predictor of phytoplankton biomass.

## Implications for lake management

Most of the shallow lakes in the temperate zone are in densely populated regions and have long been exposed to anthropogenic disturbances. These effects have become stronger recently due to the advance of intensive agriculture and recreational fishing. Although these water bodies suffer from serious nutrient loads, a reduction of nutrients does not necessarily result in the expected response of the systems (Phillips et al. 2005). This is partly attributed to the high rate of natural load of such lakes in the Carpathian Basin (Boros et al., 2008) and the high uncertainty of the nutrient–chlorophyll relationships, especially in the higher concentration range.

The lack of a relationship between land use and phytoplankton biomass has a useful message to water management, namely that the unfavourable changes in land use do not necessarily eventuate enhanced phytoplankton biomass in lakes. Nevertheless, we note that it does not mean that land use has no impact on the lakes ecosystems as a whole. Chemical fertilisers (N:50 kg $ha^{-1}$; P:5 kg $ha^{-1}$) used by the agriculture in Hungary (Anon, 2002) mean real danger for ground water quality and indirectly, contribute to the eutrophication of ground water-fed lakes. In case of these lakes (like most of the oxbows) if fish are not introduced artificially the increased nutrient content of the ground water accelerates macrophyte succession, rather than proliferation of algae. Due to this process, most of the oxbows in the Tisza valley are ageing rapidly (Pálfai, 2001).

Several studies summarised the pros and cons of food web manipulation in lake ecosystems (Benndorf, 1987; Jeppesen et al., 2007; Søndergaard et al., 2008). These studies emphasised that biomanipulation without decreasing the in-lake phosphorus holds little hope of lake quality improvement. In contrast to these results, our findings suggest that a reduction of the fish population can be a useful tool in lake management even in case of highly eutrophic conditions.

It can be concluded that favourable changes in lake use may result in the reduction of phytoplankton biomass even if land use of the surrounding area and concentration of nutrients remain basically unchanged. However, we must note that reduction of nutrients is important to ensure the long-term success of biomanipulation. Otherwise, strong fluctuations of the populations and the whole system are expected. This kind of instability was reported by Krasznai et al. (2010), who demonstrated that small hypertrophic lakes (oxbows) can be dominated by macrophytes, but the macrophyte-dominated state does not necessarily mean clear-water state, because in the small pools among the macrophytes high biomass algal blooms can occasionally develop.

Our results revealed a slight negative relationship between water depth and algal biomass. It means that artificial raising of the lake water level might be an important step in improving water quality, and this should be considered during the design and creation of artificial aquatic habitats.

## Conclusions

This study outlines the relationship between possible stressors and phytoplankton biomass in highly eutrophic shallow lakes in the Pannonian Ecoregion. We selected variables that play essential roles in phytoplankton development and developed predictive models. We showed that lake use (angling and fish stocking) and lake depth are vital in shaping phytoplankton biomass, however, we found that land use has no impact on productivity of phytoplankton in lowlands. We demonstrated that models (multiple regression, GLM and ANN models) based on lake use, lake depth, TN and TP can successfully predict phytoplankton biomass in very shallow eutrophic lakes, and that this multi-stressor approach can be proposed for the elaboration of lake management measures.

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