



A statistical model predicting the occurrence and dynamics of submerged macrophytes in shallow lakes in the Netherlands

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Abstract

Logistic regression was used to analyse the relationship between six submerged macrophyte taxa (*Chara* spp., *Potamogeton perfoliatus*, *Potamogeton pectinatus*, *Potamogeton pusillus*, *Myriophyllum spicatum*, *Alisma gramineum* and sum of all species) and four environmental variables (turbidity, effective wind fetch, water depth and sediment silt percentage, including interactions and some quadratic terms). The models were based on intensive vegetation samples (total c. 72 000) and other monitoring data carried out in five Dutch shallow lakes in the IJsselmeer area from 1988 to 1998. Water depth and light extinction were the most important factors determining the occurrence of all studied species in Veluwemeer, while effective wind fetch had a moderate effect and sediment silt had only a minor effect on the occurrence. Water depth had a negative impact on all species, except *A. gramineum*, which showed an optimum response. Three species showed an optimum response at intermediate turbidity (*M. spicatum*, *P. pusillus* and *P. pectinatus*), whereas the other taxa were negatively related. Three species (*Chara* spp., *P. perfoliatus* and *M. spicatum*) were positively related to wind fetch or showed an optimum response at intermediate value, whereas *P. pusillus*, *P. pectinatus* and *A. gramineum* were negatively related. The models including interactions between the explanatory variables showed a high goodness of fit for Veluwemeer for *Chara*, *P. pectinatus* and *M. spicatum* (in more than 8 of 10 instances, a cell originally scored '1' are predicted to have a higher probability than the ones originally scored '0'). The models of the other species showed a moderate goodness of fit (between 6 and 8 of 10 instances correctly predicted). The models developed for Veluwemeer were valid for *Chara* in all the four other lakes (more than 8 of 10 instances correctly predicted), while the models of other species were valid in some instances. A succession of vegetation was recognised based on water depth and turbidity in Veluwemeer. *P. perfoliatus* and *P. pectinatus* dominated the shallow zones under turbid conditions, but a change to dominance by *Chara* occurred in clear water. Based on the observation of co-occurrence, competition has played an important role for the shift from *P. pectinatus* to *Chara*. *Chara* became dominant 2 years after initial colonisation of *Chara* in *P. pectinatus* beds. Competition between *P. perfoliatus* and *Chara* may have been of less importance, due to a more distinct habitat (deeper colonisation) of dense *P. perfoliatus* beds. The analysed species showed large differences in vegetation stability from year-to-year. *Chara* showed the highest year to year stability (c. 65% of the cells remained covered from one year to another), while *A. gramineum* showed the highest dynamics (c. 10% of the cells remained covered from one year to another). Species producing specialized vegetative propagules for over wintering showed a higher local stability than species without such propagules.

Introduction

Submerged macrophytes are an important component in shallow lake ecosystems. They provide a habitat for zooplankton, fish and macroinvertebrates, and can be an important food source for migratory water birds (Scheffer, 1998; Noordhuis et al., 2002). Progress has

been made in research into environmental factors that affect the growth and occurrence of submerged macrophytes. Gathering this research in models provides an essential tool to get new insights on the relative importance of environmental factors (Calado & Duarte, 2000; Van Nes et al., 2002).

A number of studies have shown that the occurrence of submerged macrophytes is largely determined by water depth and water turbidity. Simple empirical models show that macrophytes colonise a maximum water depth of roughly one to two times the Secchi depth (e.g. Chambers & Kalff, 1985; Blindow, 1992a; Middelboe & Markager, 1997). Such simple models may be used to estimate the potential for vegetation extension in a lake (Canfield et al., 1985).

More sophisticated statistical models have been presented for a few species based on logistic regression (Scheffer et al., 1992; Van den Berg et al., 1999). Such models are relatively simple but they predict spatial patterns of species occurrence and the effects of changes in environmental factors. The models use turbidity and water depth as explanatory variables, sometimes combined with other factors like year averages of temperature and wind fetch. The predicted probability of presence can be translated to surface area covered by macrophytes (Scheffer et al., 1992).

Several studies have shown the importance of water depth and water turbidity for zonation patterns of submerged macrophytes (Hutchinson, 1975; Spence, 1982) or have shown large changes in the species composition when these factors change (Ozimek & Kowalczewski, 1984; Blindow, 1992b; Coops & Doef, 1996), but quantification of these spatial processes has not yet been studied in detail. Zonation patterns and vegetation shifts are supposed to be related to water depth and water turbidity (e.g. Spence & Crystal, 1970; Blindow, 1992b; Van den Berg et al., 1999). Only very few models predict such shifts in aquatic vegetation (e.g. Van Nes et al., 2002).

In Veluwemeer, the aquatic vegetation changed in response to measures implied to reduce the external phosphorus loading and the biomass of bream (*Abramis brama*) (E. Lammens, pers. comm.). Charophytes became dominant at the cost of *P. pectinatus*, probably owing to a better use of bicarbonate and higher resistance to bird grazing by *Chara* (Van den Berg et al., 2002). Although much work has been done on modelling the submerged vegetation, more studies need to be conducted on the prediction of the spatial distribution of submerged macrophytes on a species level. In addition, prediction of succession and zonation patterns are often lacking in existing models. We hypothesise that water depth and turbidity largely determine the zonation of plants in Veluwemeer. Furthermore, we hypothesise that changes in water turbidity have created succession patterns interacting with water depth.

In this study we present logistic models describing the development of six submerged macrophytes species occurring in Veluwemeer relative to four environmental factors and their interactions. We validated the calibrated models on two adjacent lakes and two neighbouring lakes. Furthermore, we analysed the role of water depth and light extinction for the succession and zonation of three dominant species in Veluwemeer and compared the year-to-year stability of six species. This paper provides validated regression models which may be helpful tools to evaluate the consequences for several submerged plant species of measures taken by the water managers, such as deepening or changing wind fetch by building dams.

Materials and methods

Study site description

We studied five lakes in a chain of very shallow freshwater lakes (1–2 m depth) situated in the IJsselmeer area (Fig. 1; see Table 1 for characteristics). The size of the lakes varies between 500 and 3050 ha and the average wind fetch ranged for most lakes between 500 and 2000 m (Table 1). The sediment consists mainly of sand and silt, but in Lake Eemmeer the sediment consists mainly of clay. They contain a regulated, seasonally changing water level (20 cm higher from March to September than the rest of the year). The lakes were formerly eutrophic and turbid. In recent years, especially in Veluwemeer and Wolderwijd, turbidity has decreased due to reduced external nutrient loading. In the clearing lakes the aquatic vegetation is dominated by charophytes (mainly *Chara aspera*, *Chara globularis*, *Chara contraria*) and *Potamogeton* spp.

Data collection and treatment

Vegetation monitoring data were collected in shallow lakes in the IJsselmeer region between 1988 and 1998. Submerged vegetation was sampled using a rake and projected cover was estimated for each species in four classes: 0, 1–15%, 16–50% and 51–100%, except for charophytes which were distinguished at the genus level. The occurrence of the six most common taxa in Veluwemeer and these taxa lumped ('sum of species') were considered in the analysis. Vegetation samples were made at 10×10 m sites located in a 100×100 m grid. Sites were located by DGPS (spatial resolution 0–2 m), which resulted in about

Table 1. Characteristics of the studied lakes

Lake	Area ha	Number of mappings	Years sampled	Water depth mean (25–75 percentiles) cm	Light extinction mean (min-max) m^{-1}	Sediment silt mean (25-75 percentiles) %	Wind fetch mean (25-75 percentiles) 10^3 m
Veluwemeer	3050	30 000	1988–1998	145 (64–219)	2.4 (1.3–3.7)	5.3 (2.25–6.5)	1.8 (1.5–2.2)
Wolderwijd	2650	25 000	1990–1998	188 (99–240)	2.4 (1.5–3.8)	4.6 (2.25–2.25)	1.9 (1.6–2.3)
Drontermeer	500	3000	1993, 1997, 1998	98 (52–105)	2.4 (2.0–3.2)	1.9 (0.75–0.75)	0.6 (0.5–1.1)
Eemmeer	1400	5000	1991, 1994, 1997	171 (117–198)	4.3 (3.9–4.8)	24 (21–30)	1.0 (0.7–1.3)
IJmeer	2800	9000	1991, 1995, 1997	136 (64–179)	2.3 (2.2–2.4)	2.3 (2.25–2.25)	2.2 (2.0–2.5)

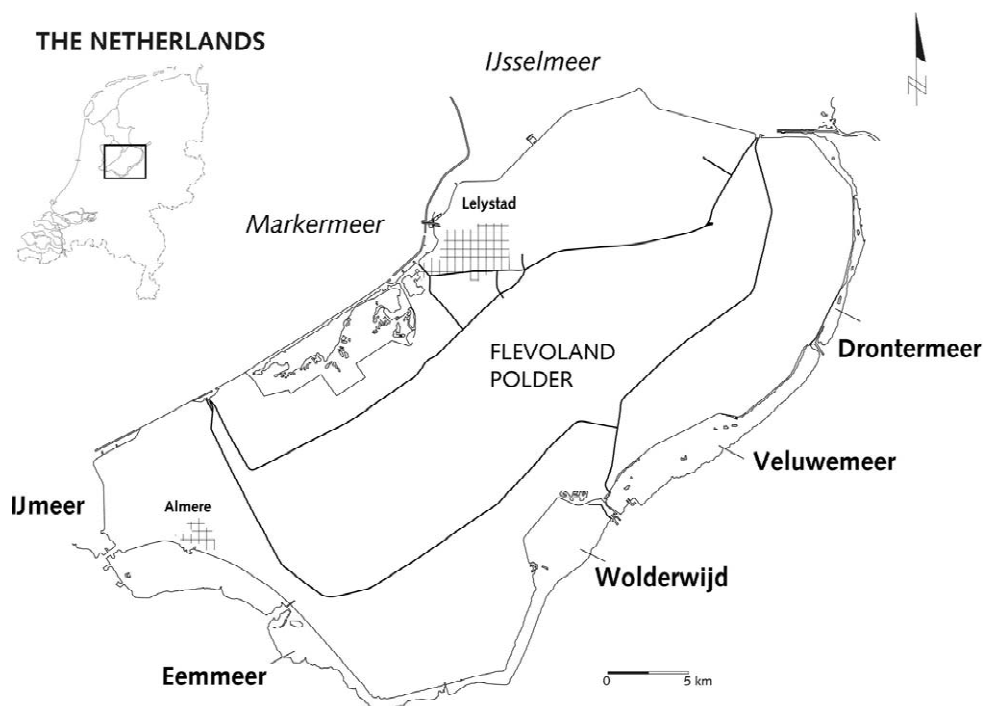


Figure 1. Map of the IJsselmeer area and locations of the studied lakes.

72 000 vegetation samples distributed over five lakes. From 1990 to 1992, only part of Veluwemeer was sampled. Two lakes (Veluwemeer and Wolderwijd) were mapped every year, while other lakes were only visited once every 3 years.

Water depth in summer elevation was measured in 1996 with at least a resolution of 100×100 m and was assumed to be constant over the years. The percentage silt of the sediment top layer (0–5 cm) was determined in 1990 and 1991 and was sampled at about six sites per km^2 . When variation was large, the sample density was increased to maximally 100 sites per km^2 . Also the sediment silt content was assumed to be constant

over the years. Effective wind fetch was calculated at all points in the lakes by measuring the distance to the shoreline in eight directions using a geographic information system (GIS). The eight distances were averaged and weighted using correction factors for the wind distribution (Scheffer et al., 1992). As a measure for water turbidity, light extinction was calculated according to Scheffer (1998) by using averages of inverse Secchi depth (Z_s) and chlorophyll-*a* concentrations from weekly to monthly data sampled one site in each lake between 15 April to 15 October:

$$\text{turbidity} = 0.016 * \text{chlorophyll} - a + 0.46 / Z_s^{0.5} \quad (1)$$

The macrophyte data and water depth data were interpolated using a GIS application using a 10×10 m grid. For interpolation of data an inverse distance weighting method was used with a search radius of 150 m and an interpolation power of 2. Because vegetation was not sampled exactly at the same location each year the interpolated maps were used for further data processing. The map of silt data were visually interpolated by expert judgement, because of limited data quantity. All grids were combined into a new data set for which 1% of the grid data were selected to reduce the number of data. The final number of grid cells in the analysis (46 972) was less than the original number of vegetation sampling points (c. 72 000). For the statistical analysis software of SPSS (SPSS Inc.) was used.

Independency of explanatory variables

The explanatory variables were tested for their independence using a Pearson product moment correlation test (Table 2). Most variables showed a low correlation coefficient ($r < 0.16$) indicating that they are more or less independent. Only water depth and sediment silt content showed a moderate correlation (0.58), indicating that differences in effects of water depth and silt content on occurrence of macrophytes may be difficult to unravel. Turbidity was correlated with time. The transparency has gradually improved over the past 10 years.

Logistic modelling

Logistic regression (e.g. Jongman et al., 1995) was used to predict the probability of vegetation in a grid cell. The general expression for this probability is:

$$P(x) = \frac{\exp(b_0 + b_1x_1 + b_2x_2^2 \dots)}{(b_0 + b_1x_1 + b_2x_2^2 \dots)} \quad (2)$$

where b_0 , b_1 and b_2 are regression coefficients with b_0 as constant term. The parameters (b_0 , b_1 and b_2) are estimated by the maximum likelihood principle. The x value represents the explanatory variable. The resulting curve produces a sigmoidal increase or decrease in the probability of occurrence. More explanatory variables can be added. In our case we also included quadratic and interaction terms of variables by which more elaborate models can be fitted, such as maxima or minima in occurrence of species. Quadratic terms were only included in the model when a maximum or

a minimum was predicted. For criteria, see Jongman et al. (1995).

We first modelled the occurrence (presence or absence) of six species and the sum of these species in Lake Veluwemeer using the four factors: water depth (cm), turbidity (m^{-1}), silt percentage (%) and wind fetch (m). At first we considered only the strength and direction of factors and their quadratic terms on species occurrence. For this purpose, a partial correlation coefficient (r) between dependent and each independent variable was calculated as:

$$r = \pm(\text{Wald statistic} - 2K / -2 \log \text{likelihood})^{0.5} \quad (3)$$

The Wald statistic is calculated by the square of the ratio of the estimated coefficient to its standard error. The K represents the degrees of freedom of the independent variable. The log likelihood is calculated considering a model fitted on data containing only an intercept. The r value ranges between -1 and 1 and represents the direction and strength of the effect on the likelihood of the event occurring, whereby a correction is made for the scale of differences of independent variables.

Secondly, the parameter estimations of logistic models were determined using all significant variables of the first step, but including all interactions between the factors. A backward removal process of variables was followed, according to their contribution to the final results as measured when using the maximum likelihood with a critical level of significance $P < 0.1$.

The goodness of fit of the model was examined by calculating the so-called Area Under Curve (AUC) value. For an extended example, see Fielding & Bell (1997) or Cumming (2000). The AUC value represents the goodness of fit over the whole range of predicted and observed probabilities. In short, this method is based on classification of the predicted and observed cases above and below 10 cut levels of probabilities (0.05, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9). The cumulative number of positives are counted above (count a) and below each p -cut off (value c). In addition, the cumulative number of negatives are counted above (value b) and below the p -cut-off (value d). The 1-specificity of the model is defined as:

$$b/(b + d) \quad (4)$$

and the sensitivity is defined as:

$$a/(a + c) \quad (5)$$

The sensitivity and 1-specificity (x -axis) were plotted against each other. This results in a so-called Receiver

Table 2. Pearson correlation coefficients between variables possibly affecting the occurrence of aquatic plants in Veluwemeer, 1988–2000, $n=23844$

	Time	Extinction	Water depth	Wind fetch
Time	–			
Extinction	–0.75	–		
Water depth	–0.14	0.07	–	
Wind fetch	0.08	–0.04	–0.16	–
Silt content	0.11	–0.06	–0.58	–0.06

Operating Characteristics (ROC) plot showing a curve starting in (0,0) and ending in (1,1). The AUC value was determined in 11 steps and summed. The AUC value gives an easily interpretable goodness of fit of models. For example, an AUC value of 0.8 indicates that in 8 of 10 instances, a cell selected at random from the group of those originally scored '1' had a higher predicted probability than a cell selected at random from the group originally scored '0' (Fielding & Bell, 1997; Cumming, 2000). The calibrated models for Lake Veluwemeer were validated on other lakes in the IJsselmeer area. The AUC value cannot be calculated for lakes when a species was absent, while the predictions might be useful. To avoid this problem, a low number of presence cases (0.1) was added to each cut level.

Results

Importance of factors for macrophytes

Water depth and light extinction were the most important factors explaining the occurrence of aquatic macrophytes in Veluwemeer (Table 3). For all species, except for *A. gramineum*, water depth had a negative impact on their occurrence. *A. gramineum* showed an optimum response at intermediate water depth. The occurrence of three taxa and the sum of species were negatively related to light extinction. Three species (*M. spicatum*, *A. gramineum* and *P. pectinatus*) showed an optimum response to light attenuation. Effective wind fetch was generally ranked as the third most important factor. The direction of the effect differed between the species. The occurrence of *Chara* spp. was positively affected by a high effective wind fetch and *P. perfoliatus* and *M. spicatum* showed an optimum response. On the other hand, the occurrence of *P. pusillus*, *P. pectinatus* and *A. gramineum*

was negatively related to wind fetch. The silt content of the sediment was generally of minor importance for the occurrence of submerged macrophytes. Most species were favoured by a higher silt content of the sediment, except *P. perfoliatus*, which occurred more frequently at a lower silt content.

Complete logistic models for Veluwemeer

The parameter estimations of complete models for predicting the occurrence of species in Veluwemeer are presented in Table 4. All species were significantly affected by four or more interaction terms of environmental factors. Although these models produced a statistically better fit than models without interaction terms, interpretation of the models is difficult. The role of interaction terms is visualised for *Chara* in Figure 2 by showing frequencies of occurrence for a complete water depth, extinction and wind fetch gradient. The occurrence of *Chara* decreased with water depth. The frequency of occurrence, as well as the colonised water depth, was much higher in years with clear water (turbidity between 1 and 2 m^{-1}) than in years with more turbid water (light extinction >2). The effect of extinction was dependent on water depth, explaining the interaction between water depth and extinction (Table 3). Wind fetch had a positive effect on the occurrence of *Chara*. However, this effect was only pronounced in the shallow areas. Accordingly, the interaction term between wind fetch and water depth appeared significant (Table 3). In general, the fitted responses match the observed frequency distributions. As an exception, the model predicted higher probabilities of *Chara* occurrence at shallow sites than evidenced by the occurrence in the field. This is due to a low number of cells with water depths less than 0.5 m in the data set by so that the modelled pattern was mainly affected by sites somewhat deeper.

Table 3. Strength and direction of effect of explanatory variables and their quadrates at the probability of occurrence of six aquatic macrophyte species expressed in a standardised r -value between -1 and 1

Taxa	Water depth	Turbidity	Fetch	Sediment	Water depth ²	Turbidity ²	Fetch ²
<i>Chara</i> spp.	-0.32	-0.37	0.13	0.01	n.s.	n.s.	n.s.
<i>P. pectinatus</i>	-0.25	0.07	-0.10	0.03	n.s.	-0.05	n.s.
<i>P. perfoliatus</i>	-0.08	0.10	0.03	-0.04	n.s.	n.s.	-0.035
<i>P. pusillus</i>	-0.22	-0.13	-0.13	0.02	n.s.	n.s.	n.s.
<i>M. spicatum</i>	-0.21	0.16	0.03	0.02	n.s.	-0.15	-0.05
<i>A. gramineum</i>	0.12	0.09	-0.11	0.09	-0.13	-0.09	n.s.
Sum of species	-0.39	-0.24	-0.04	n.s.	n.s.	n.s.	n.s.

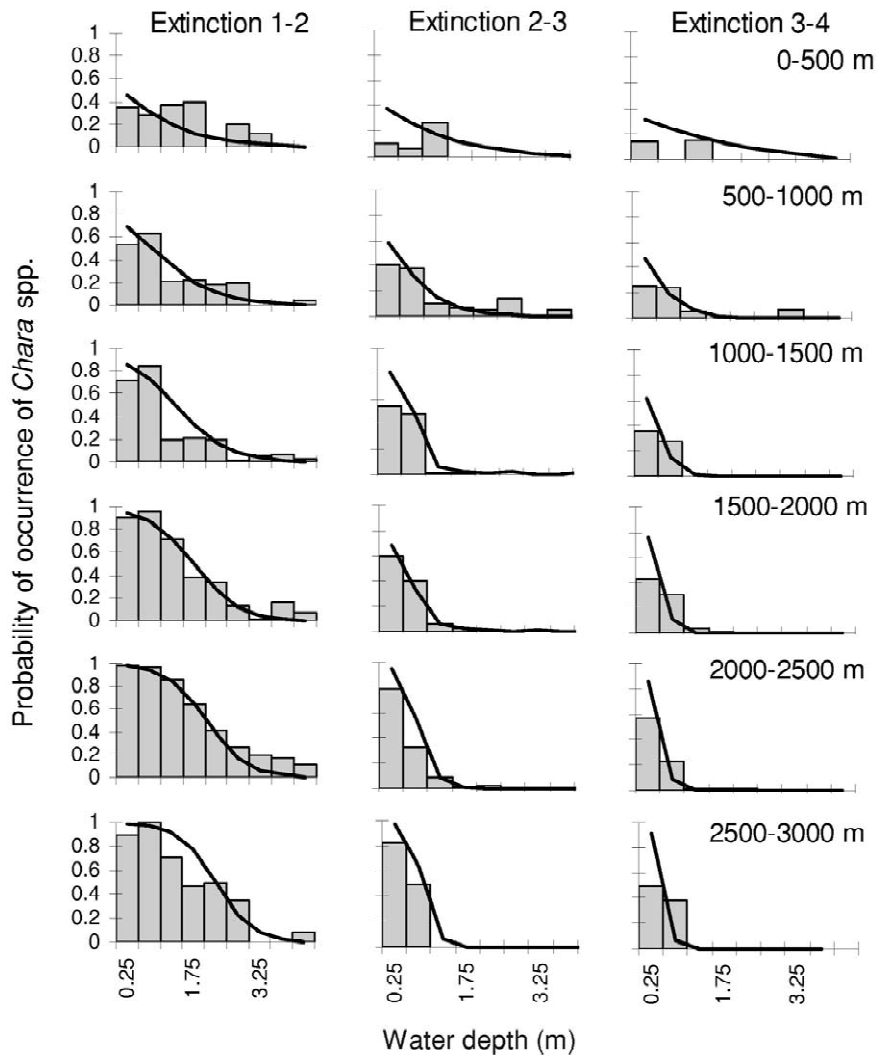


Figure 2. Frequency of occurrence (bars) and modelled response (lines) of *Chara* in Lake Veluwemeer for different combinations of classes of water depth (x -axis), wind fetch (rows) and light extinction (columns).

Table 4. Parameter estimations of logistic models for different taxa occurring in Veluwemeer 1988–1998. Only significant factors and their interaction terms of Table 2 were included in the model ($P < 0.1$)

Factor	<i>Chara</i> spp.	<i>P. pectinatus</i>	<i>P. perfoliatus</i>	<i>P. pusillus</i>	<i>M. spicatum</i>	<i>A. gramineum</i>	Sum of species
Water depth (Wa)	-0.024	-0.046	0.0037	-0.060	-0.034	0.046	-0.018
Turbidity (Tu)	-0.36	1.4	n.s.	-2.1	5.5	2.9	-1.1
Fetch (Fe)	0.0023	-0.0046	-0.0009	-0.0042	-0.0011	-0.0042	n.s.
Sediment (Se)	0.12	-0.16	0.051	0.23	-0.23	-0.69	n.s.
Water depth ²						-0.0004	
Turbidity ²		-0.43			-1.0	-0.84	
Fetch ²			n.s.		-5.8 10 ⁻⁷		
Wa*Tu	0.0084	0.0095	0.0018	0.019	0.0069	0.012	0.005
Wa*Fe	2.4 10 ⁻⁵	4.3 10 ⁻⁵	5.3 10 ⁻⁶	4.4 10 ⁻⁵	3.2 10 ⁻⁵	3.7 10 ⁻⁵	5.1 10 ⁻⁶
Wa*Se	n.s.	0.0008	-0.0003	0.0006	0.0011	0.0044	n.s.
Tu*Fe	n.s.	0.0018	0.0007	0.0019	0.0009	0.0010	0.0003
Tu*Se	-0.06	n.s.	n.s.	-0.16	n.s.	n.s.	n.s.
Fe*Se	-0.0002	8.3 10 ⁻⁵	n.s.	-0.0002	0.0002	0.0003	n.s.
Wa*Tu*Fe	-1.9 10 ⁻⁵	-2.2 10 ⁻⁵	-5.0 10 ⁻⁶	-2.7 10 ⁻⁵	-1.4 10 ⁻⁵	-1.3 10 ⁻⁵	-4.7 10 ⁻⁶
Wa*Fe*Se	n.s.	-6.8 10 ⁻⁷	-5.4 10 ⁻⁸	n.s.	-1.2 10 ⁻⁶	-1.1 10 ⁻⁶	n.s.
Ex*Fe*Se	8.12 10 ⁻⁵	n.s.	-2.3 10 ⁻⁵	9.3 10 ⁻⁵	n.s.	7.2 10 ⁻⁵	n.s.
Wa*Tu*Fe*Se	7.78 10 ⁻⁸	2.3 10 ⁻⁷	1.2 10 ⁻⁷	n.s.	1.5 10 ⁻⁷	-5.5 10 ⁻⁷	n.s.
Constant	-0.015	1.5	-1.8	5.1	-7.3	-6.5	4.47

Model calibration and validation

The goodness of fit values of the complete models of Veluwemeer (Table 4) are presented as AUC values in Table 5. The models were calibrated for Veluwemeer and most species showed a high AUC value. Especially, the models for *Chara*, *P. pectinatus*, *M. spicatum* and the sum of species showed a good fit by giving AUC values higher than 0.80. For those species, in at least 8 of 10 instances, a random cell originally scored '1' is predicted to have a higher probability than a random cell originally scored '0'. The goodness of fit of *P. perfoliatus*, *P. pusillus* and *A. gramineum* was moderate with AUC values between 0.63 and 0.70. In general, a high goodness of fit corresponded to frequently occurring species.

For *Chara* spp. the calibrated model of Veluwemeer was also valid for other lakes in the IJsselmeer area. The AUC values ranged between 0.79 for Drontermeer and 0.99 for IJmeer. The models for *M. spicatum* and *A. gramineum* were valid for other lakes but only for lakes where the species were not present (AUC values higher than 0.8). In Drontermeer, where both species were present, the validation was moderate for *A. gramineum* (0.74) and below random expectation for *M. spicatum* (0.45). Based on the Veluwemeer models,

the absence of *M. spicatum* and *A. gramineum* was well understood in other lakes, but the models were inaccurate for predicting their presence. The models of *P. pectinatus* and *P. perfoliatus* showed a poor to good fit for other lakes. The AUC value ranged between 0.62 and 0.77 for *P. pectinatus* and between 0.53 and 0.76 for *P. perfoliatus*. For *P. pectinatus*, the fit was good for the adjacent lakes Wolderwijd and Drontermeer, while a moderate fit was found for IJmeer and Eemmeer, lakes situated at some distance. The Veluwemeer model of *P. pusillus* was valid for Drontermeer, where it dominated the vegetation. However, the fit of the *P. pusillus* model was poor for lakes in which the species was less common, such as Eemmeer and IJmeer.

A spatial example of the goodness of fit of the complete Veluwemeer model is presented for *Chara* in clear water conditions for Veluwemeer and Wolderwijd (Fig. 3). The overlap in predicted probabilities and vegetation presence is obvious for both lakes. In general the predicted probabilities were higher at sites where the vegetation was more dense.

Vegetation stability

From 1988 to 1998 the spatial stability of vegetation from year-to-year at a site differed for species in-

Table 5. Goodness of fit of logistic models predicting the occurrence of six taxa calibrated on Veluwemeer ($n=23\ 589$, 11 years) and validated on Wolderwijd ($n=14\ 112$, 9 years), Drontermeer ($n=1247$, 3 years), Eemmeer ($n=3100$, 3 years) and IJmeer ($n=3037$, 3 years) expressed as AUC values. The percentage of presence cases (% 1) in the data set is presented per lake and per species, a means absent

Taxa	Veluwemeer		Wolderwijd		Drontermeer		Eemmeer		IJmeer	
	AUC	%1	AUC	%1	AUC	%1	AUC	%1	AUC	%1
<i>Chara</i> spp.	0.90	37	0.87	26	0.79	28	0.93	a	0.99	2
<i>P. pectinatus</i>	0.85	18	0.77	17	0.76	25	0.62	6	0.62	11
<i>P. perfoliatus</i>	0.70	26	0.67	30	0.53	23	0.76	0	0.60	13
<i>P. pusillus</i>	0.63	5	0.62	6	0.74	37	0.50	0	0.51	4
<i>M. spicatum</i>	0.83	12	0.89	a	0.45	31	0.92	a	0.92	a
<i>A. gramineum</i>	0.68	2	0.94	a	0.74	1	0.96	a	0.80	a
Sum of species	0.86	63	0.85	55	0.89	79	0.72	14	0.78	28

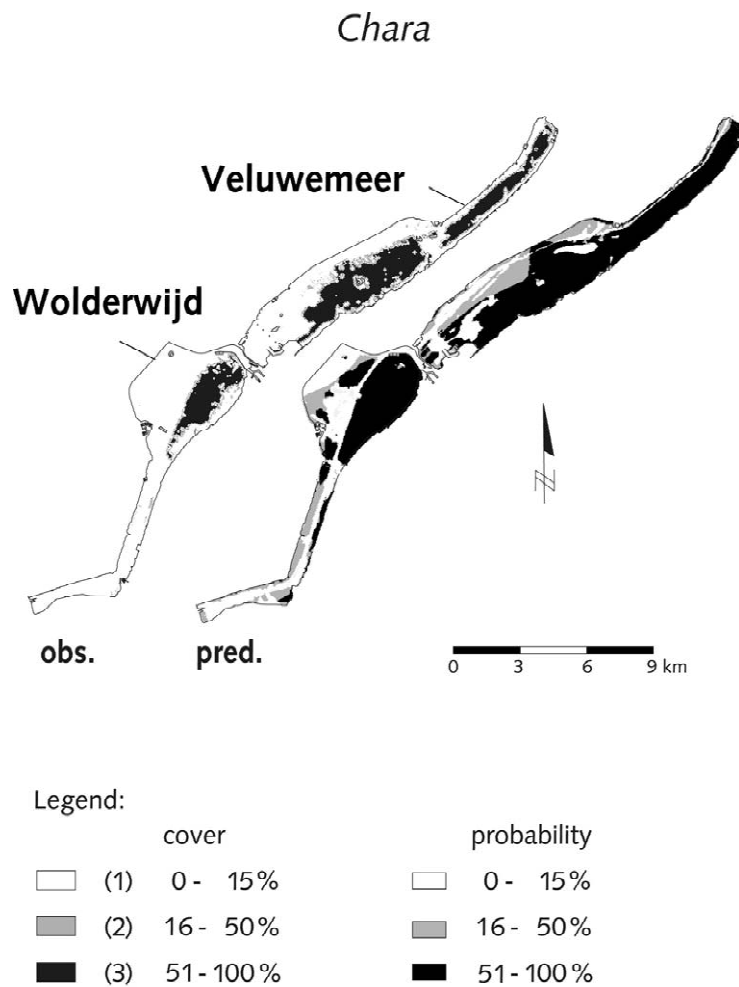


Figure 3. Example of an observed vegetation map, interpolated using GIS (obs.) in comparison to its predicted response (pred.) of *Chara* spp. in a clear situation in Veluwemeer (extinction 1.3) and Wolderwijd (extinction 1.4).

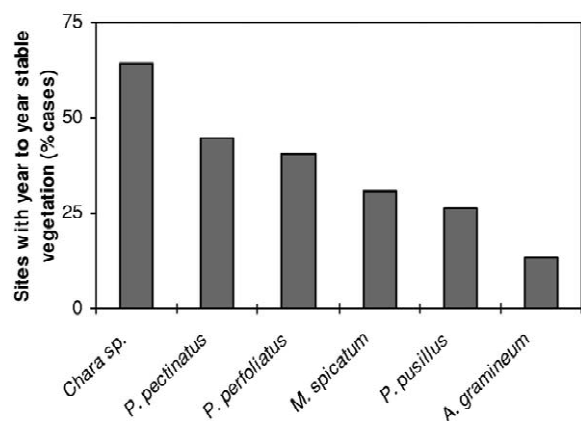


Figure 4. Year-to-year appearance of *Chara* and disappearance of *P. pectinatus* in Veluwemeer from 1988 to 1998 for different combinations of vegetation change.

involved (Fig. 4). *Chara* formed a very stable vegetation throughout the past 10 years. About 65% of the sites covered by *Chara* in 1 year remained covered in the next year, while at 5% of the sites vegetation disappeared and at c. 30% of the sites new stands emerged. *A. gramineum* showed the highest interannual variability. At only 10% of the sites where this species was present, it remained present in the subsequent year. The other species responded intermediately.

Zonation and successional patterns in Veluwemeer

The probability of occurrence of species density classes can be described as the function of water depth and extinction by a logistic model (Table 6). For all three species the probability differed slightly for different density classes (Fig. 5). Dense *Chara* vegetation showed an optimum response to water depth in clear water, while open vegetation showed an increasing probability of occurrence with increasing shallowness. In addition, dense *Chara* vegetation was overall more likely to occur compared to open vegetation (respectively 85% vs. 25% maximum). The occurrence of open *P. pectinatus* vegetation (coverage 1–15%) was concentrated at shallow parts and showed an optimum to turbidity. Dense vegetation (15–50% coverage), in contrast, showed no such response to turbidity and occurred also at deeper parts. The responses of different density classes of *P. perfoliatus* to water depth and extinction were more or less similar, although dense vegetation showed an increasing probability at higher water depth. *P. perfoliatus* showed large tolerances to water depth and turbidity.

The presented species showed different responses to water depth and extinction (Table 6). A succession of species in response to water depth and extinction was observed since Veluwemeer changed from turbid (1988, extinction 3.8) to clear (1998, extinction 1.3). In a turbid year the predicted occurrence of macrophytes at a depth of 50 cm was dominated by *P. perfoliatus* (total frequency 85%) followed by *P. pectinatus* (frequency 32%) and *Chara* (frequency 25%; Fig. 5, Table 6). In turbid water, the occurrence of *Chara* and *P. pectinatus* at deeper parts (3 m) was less than 2%, while *P. perfoliatus* showed a probability of c. 20% at this water depth. In a year with clear water (1998: extinction 1.3) the pattern was completely different. Charophytes dominated the shallow zones (frequency 92%), while *P. perfoliatus* (frequency 0.17) and *P. pectinatus* (0.14) declined compared to the turbid situation. In deeper parts (c. 3 m), *Chara* and *P. perfoliatus* dominated the vegetation (frequency respectively 0.29 and 0.23), while *P. perfoliatus* showed the greatest colonisation depth.

During succession, the year-to-year vegetation dynamics of *P. pectinatus* and *Chara* were strongly interrelated (Fig. 6). Yearly appearance of *Chara* varied strongly over the years (between 4 and 26% of the cells). Between 1988 and 1991 most of the new cells colonised by *Chara* were those where *P. pectinatus* grew previously. The most significant colonisation took place in 1990, although this is probably overestimated in absolute terms because only part of the lake was mapped with abundant vegetation. From 1995 onwards, colonisation of *Chara* mainly occurred at sites without *P. pectinatus*. The disappearance of *P. pectinatus* during the first years of *Chara* colonisation was mainly at sites without *Chara*, though a remarkably high number of cells with *P. pectinatus* disappeared in 1992 and 1993 at sites with stable *Chara* about 2 years later than the strong colonisation of *Chara* inside the *P. pectinatus* stands. From 1994 onwards, disappearance of *P. pectinatus* was slower and took place mainly at sites with *Chara*. Co-existence of other species with *Chara* occurred in between 40 and 80% of the cells (Fig. 7). This suggests that interactions as observed for *P. pectinatus* may occur for other species too. Only *P. perfoliatus* showed *Chara* co-occurrence a relatively low number of cells.

Table 6. Parameter estimates of logistic models for different densities of cover for three species occurring in Veluwemeer 1988–1998 based on water depth and extinction

Species	Cover class %	Factor							AUC
		Water depth	Turbidity	Water depth ²	Turbidity ²	Water depth* Turbidity	Constant		
<i>Chara</i> spp.	1–14	0.018	0.63	n.s.	n.s.	–0.014	–2.0	0.69	
	15–100	0.053	0.59	$-7.8 \cdot 10^{-5}$	n.s.	–0.030	–0.53	0.86	
<i>P. pectinatus</i>	1–14	0.0046	3.4	n.s.	–0.45	–0.012	–4.8	0.82	
	15–100	0.038	2.8	n.s.	n.s.	–0.028	–8.5	0.75	
<i>P. perfoliatus</i>	1–14	0.0057	1.5	n.s.	–0.12	–0.0042	–3.5	0.66	
	15–100	0.028	1.2	$-2.8 \cdot 10^{-5}$	n.s.	–0.0081	–7.2	0.63	

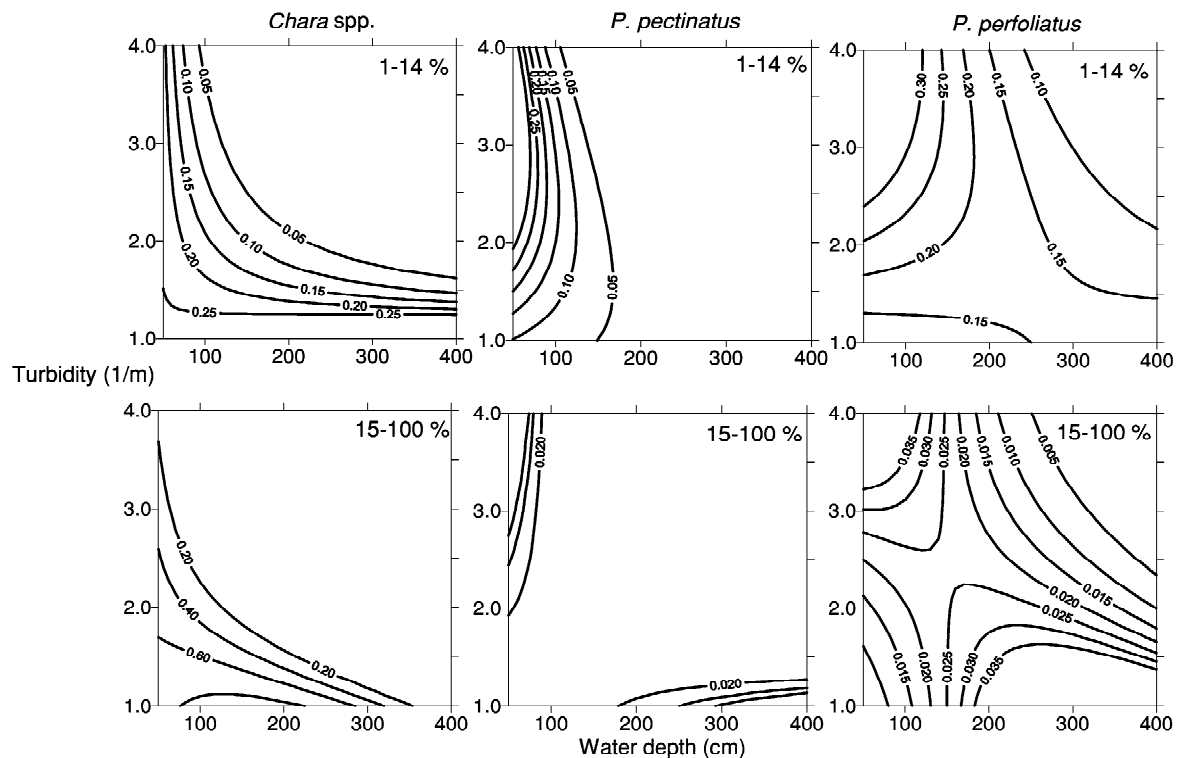


Figure 5. Modelled response presented as isoclines of probability for three dominant species and two density classes to water depth and light extinction in Lake Veluwemeer 1988–1998. The models are presented in Table 6.

Discussion

Logistic regression is useful for describing the spatial distribution of submerged macrophyte species. The calibrated models in this study showed a high goodness of fit for at least three taxa and the sum of species. Notably, for some species the models produced from Veluwemeer data were often valid for similar lakes in the vicinity. Other studies have shown that logistic

regression is not very appropriate to predict vegetation presence (Scheffer et al., 1992; Van den Berg et al., 1999). In our case, however, we showed that the likelihood of vegetation presence can be predicted well for most species by using a sophisticated test for goodness of fit of the models. The use of AUC values for goodness of fit takes into account that input data containing low presence cases result in lower predicted maximum probabilities, and therefore can

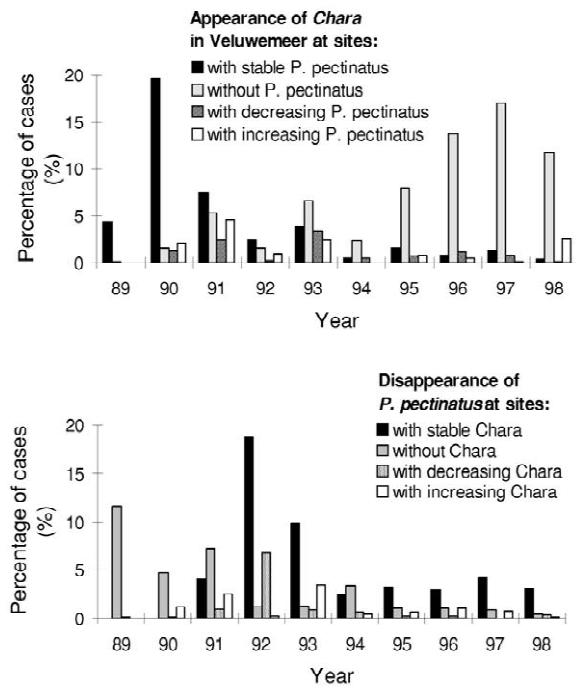


Figure 6. Year to year vegetation stability expressed as the percentage of sites with remaining vegetation of eight species occurring in the IJsselmeer area based on an interpolated vegetation grid cell size 10×10 m).

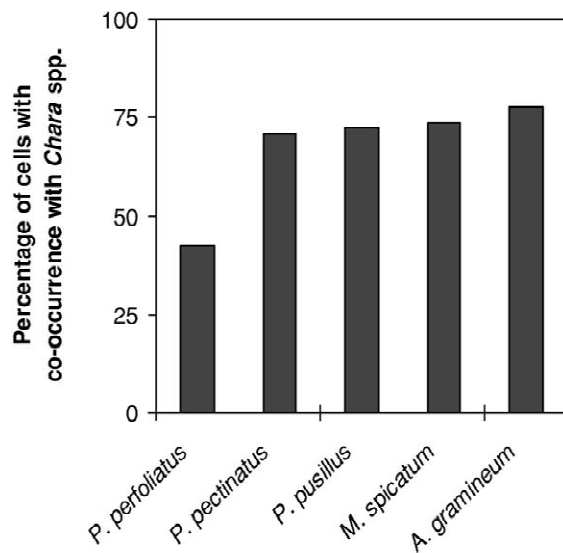


Figure 7. Co-occurrence of different species in *Chara* vegetation in Veluwemeer 1991–1998.

detect the model prediction where presence is most likely to occur (Cumming, 2000). Using the presented models, small changes in lake morphology or changes in wind fetch (e.g. by building dams) may be quantitatively evaluated. The models were, however, not valid under all circumstances and for all species, implying that other factors in addition to those included in the model play a significant role in determining vegetation occurrence. Another important limitation of the logistic models is that they do not account for feedback mechanisms between vegetation and environment. Particularly, the feedback of vegetation on turbidity (e.g. Jeppesen et al., 1990; Scheffer, 1998; Portielje & Rijsdijk, accepted for publication) strongly affects the response of aquatic vegetation to changes in turbidity and may lead to discontinuous responses to changes in the turbidity (Scheffer et al., 1993), a fact that these models do not take into account.

Water depth and light extinction were the most important factors determining the occurrence of submerged vegetation. This is in agreement with other studies on the relative importance of environmental factors for the dynamics of aquatic macrophytes (Scheffer et al., 1992; Rea et al., 1998). Also, very shallow water was not favourable for the occurrence of submerged macrophytes. For most species, however, too few data from cells shallower than c. 0.3 m were available to allow the models to be extended over the entire depth gradient. At such shallow sites, the development of submerged macrophytes may be hampered due to limited space for growing, faster exhaustion of nutrients such as dissolved inorganic carbon or higher wave action (e.g. Scheffer et al., 1992).

Experimental studies have shown that sediment may have a strong effect on the occurrence of aquatic macrophytes through toxic substances and nutrient limitation (Smolders & Roelofs, 1993; Best et al., 1996) or via organic matter content (Barko & Smart, 1983). Our study showed that the silt content of the sediment was relatively less important in explaining the spatial occurrence of submerged macrophytes. Other 'within' lake studies also showed a minor effect of sediment type on the distribution pattern of submerged macrophytes (Remillard & Welch, 1993; Weisner et al., 1997). Water depth, however, might mask part of the effect of sediment because these factors may be correlated, as was the case in our study. Additionally, we did study only a few sediment characteristics (e.g. organic matter content or grain size), so that effect of sediment also may be hidden. This restricts the extrapolation of models developed for

lakes with mineral sediments (organic matter content generally below 1% of dry weight).

Wind fetch may have positive and negative effects on the occurrence of submerged macrophytes. A strong wave action due to long wind fetches may induce mechanical damage to the plants (Schutten & Davy, 2000), but it may as well be an advantage because of removal of periphyton which otherwise causes light attenuation (Scheffer et al., 1992; Weisner et al., 1997). In our study, the effect of fetch was not identical for all species. *Chara* showed a positive correlation with fetch, while *P. pectinatus*, *P. pusillus* and *A. gramineum* occurred more frequently at sites with a low fetch. This species-specific correlation may be due to differences in physical strength because macrophytes have a specific hydraulic resistances (Schutten & Davy, 2000). Charophytes may be highly resistant to hydraulic forces caused by wind induced waves, because of their low individual weight and their massive bottom covering growth form.

In the course of several years, the species showed different responses to changes in water clarity. When the water became more clear *Chara* started to colonise inside *P. pectinatus* beds and *P. pectinatus* disappeared mainly from sites where *Chara* had settled. The gradual replacement of *P. pectinatus* may have taken c. 2 years. Similar shifts between *Chara* and *P. pectinatus* have been observed in other lakes, but the mechanisms are unknown (Blindow, 1992b). Several authors stress the importance of interspecific competition in submerged macrophytes beds under laboratory conditions (Moen & Cohen, 1989; Spencer & Rejmanek, 1989) and competition is also suggested to affect zonation patterns (Hutchinson, 1975). Our results show that co-occurrence is very common among submerged macrophytes and suggests the importance of inter-specific competition for vegetation dominance. This implies that interspecific competition is very likely to occur, which is in agreement with experimental studies carried out in the laboratory (Van den Berg et al., 1998). Interspecific competition between *Chara* and other species also plays an important role given the high number of cases showing co-occurrence. However, some species tend to colonise habitats slightly different from *Chara* due to different preferences for wind fetch or water depth. For example *P. perfoliatus* showed a distinct habitat from *Chara* by occurring at greater water depths. In addition, *P. pectinatus* dominated the shallow and wind sheltered parts and dominated especially under turbid conditions. In case of the *P. perfoliatus*–*Chara*

interaction, interspecific competition may be of relatively low importance considering the low number of shared grid cells.

The observed succession patterns can be statistically analysed using logistic models which then may be used for predicting vegetation densities. The mechanisms behind the succession are, however, not taken into account. This limits their use for prediction. A method to explore the role of competition in vegetation patterns is the use of deterministic models. One such model, Charisma (Van Nes et al., 2002; Van Nes et al., 2003) shows that the recolonization of *Chara* as occurred in Veluwemeer was not well simulated, unless an extra loss factor (such as bird grazing) is introduced for *P. pectinatus*. Water birds may also prevent re-establishment of *P. pectinatus*, because birds may use tubers as food source alternative to *Chara* resulting in a much lower tuber density than in the absence of such an alternative food source (Noordhuis et al., 2002).

Local stability from year to year varies among species. The most stable species occurring in our lakes returned in 50–65% of the cases in the same cell (10×10 m, based on interpolation), implying that each year 35–50% of the stands disappear or appear at another site. The high spatial instability is in agreement with Scheffer et al. (1992) who showed strong local dynamics of *P. perfoliatus* and *P. pectinatus* in the same lakes in the period 1969–1987. The propagule bank plays an important role in the year to year dynamics of aquatic macrophytes (Van den Berg et al., 1999) and ensures the first precondition for return at the same site in the following year. Charophytes form both bulbils and bird grazing resistant oospores in large amounts (total about 20% of DW), which may partly explain their stability. At first sight the high stability of *Chara* vegetation contradicts the notion that *Chara* is a typical pioneer (Wade, 1990) and therefore forms un-stable plant communities. We showed, however, that *Chara* vegetation is relatively stable and is highly competitive too.

In conclusion, logistic models can be used predict the probability of submerged macrophytes on a species level. They can be helpful tools to evaluate the consequences for several submerged plant species of measures taken by the water managers. Furthermore, analysis of the data beyond the models provides new insights in dynamics of submerged macrophytes such as stability of species, zonation and succession patterns.

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