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STRUCTURE OF SUBMERGED LITTORAL VEGETATION IN RELATION TO PELAGIC TROPHIC STATE INDICES

ABSTRACT: An attempt was undertaken to compare pelagic indices commonly used to describe trophic status of lakes (SD, chlorophyll, total phosphorus and total nitrogen) with parameters characterising submerged littoral zone of lakes (maximum depth of plant occurrence, number of species, mean plant biomass and percentage biomass of the dominating species). The data were collected from 20 lakes of various morphometry and trophic state selected from the Great Masurian Lakes system (north-eastern Poland) from 1985 till 1995. The greatest impact on submerged littoral structure (species abundance and diversity) was exerted by water transparency, nutrient concentrations had negligible effect on littoral parameters. From among four littoral characteristics, submerged plant biomass seems to be of the poorest indicative value since its correlation with pelagic indices was usually weakest and statistically insignificant.

KEY WORDS: lake littoral, submerged macrophytes, species composition, nutrients, chlorophyll, water transparency

1. INTRODUCTION

Submerged aquatic macrophytes may serve as a good indicator of the human impact on lake ecosystem. First to be affected by the land inputs, macrophytes have a potential to reflect spatial and temporal environmental variability both by the changes in biomass and in the species composition of the whole community (Seddon 1972, Ozimek 1978, Pieczyńska et al. 1988, Duarte and Kalff 1990). There is no, however, simple relationship between concentration of pollutant and/or nutrient and the biomass of any submerged species. The relationships are even more complex when the whole plant assemblages are taken as indicative parameters. Utilisation of the substratum and lake water as a source of nutrient supply make the plants susceptible to both the local (littoral) and the whole-lake degradation. Except for the inorganic nutrient uptake, macrophyte growth depends on the site-specific characteristics like composition of substratum (Barko and Smart 1986), littoral slope (Duarte and Kalff 1986), water level fluctuations and light attenuation (Blindow 1992), exposition to waves etc. The influence of changing environmental factors on macrophyte biomass is linear only within a limited range of variability, further on the response of macrophyte community is realised by the rearrangement of species composition. Submerged macrophytes which are typical for mesotrophic conditions are replaced by more eurytopic species and finally macrophytes give way to planktonic algae as it is often the case in highly eutrophic shallow lakes (Blindow et al. 1993, Scheffer et al. 1993).

All these factors make the application of higher aquatic plant for monitoring purposes dubious (Lewis 1995) and point to the need of extended research on the relationships between pelagic and littoral indices. This work was undertaken to compare commonly used pelagic trophic state indices with some characteristic features of the submerged littoral.

2. MATERIALS AND METHODS

Samples were collected from 20 lakes of various morphometry and trophic status in the Great Masurian Lakes system (north-eastern Poland – Table 1). All lakes are interconnected through the system of channels. Main sources of the land impact on lakes are agriculture, domestic sewage and tourist activity in summer. Lakes are to a different degree affected by the human activity, so there are polytrophic as well as mesotrophic lakes within the system.

Water samples were taken at a depth of 1 m from the deepest part of lakes during summer stagnation period. Chlorophyll *a* (Chl) was determined by the spectrophotometric analysis of acetone extracts of algae retained on Whatman GF/C filters (Golterman 1969). Total phosphorus was analysed in unfiltered water samples after wet digestion with perchloric acid (1 ml of acid/50 ml of sample) by spectrophotometric determination according to Standard Methods (1960). Kjeldahl nitrogen was analysed in unfiltered water samples by the standard Kjeldahl procedure. Resulting ammonia was measured by phenate method of Solórzano (1969) with minor modifications. Nitrate-nitrogen was analysed by phenyldisulphonic method (Standard Methods 1960) from filtered (Whatman GF/C) lake water. Sum of Kjeldahl nitrogen and nitrate-nitrogen concentrations represented total nitrogen (TN) in lake waters. All chemical analyses were triplicated.

Samples of submerged plants were taken along transects (same for the whole sampling period in order to avoid site-specific variability) laid out from the border of reed belts lakeward to the maximum depth (D_{max}) of plant occurrence, every 0.5 m of the depth increment. Plants were harvested with a grab sampler of an area of 0.16 m^2. Species composition was determined in plant samples and, after drying at 105° C, dry weight of plants was measured for each sampling point. For further calculations number of species found in the transects (N), dry weight of plants (DW) averaged over the whole transect and percentage share of the dominating species (%Dom) in the total biomass were used as the littoral indices.

Table 1. Morphometric and trophic characteristics of the sampled lakes

Lake	Area (ha)	Max. depth (m)	Mean depth (m)	Mictic type	Trophic status	Sampling period
Przystań	500	45.6	–	d	m	1985, 1988, 1993–1995
Mamry	2004	47.0	11.7	d	m	1985, 1988, 1991–1993, 1995
Święcajty	813	28.0	10.2	d	e	1985, 1993–1995
Dargin	3030	37.6	10.6	d	m-e	1985, 1993
Kisajno	1896	25.0	8.4	d	e	1985, 1991, 1993–1994
Niegocin	2600	39.7	10.0	d	pt	1985, 1988, 1991–1994
Boczne	183	17.0	8.7	d	e	1985
Jagodne	943	37.4	8.7	d	e	1985, 1993–1994
Tałtowisko	327	39.5	14.0	d	e	1993
Tałty	1162	37.5	13.6	d	e	1985, 1988, 1991–1995
Ryńskie	620	47.0	13.6	d	e	1985, 1988, 1992–1995
Mikołajskie	497	25.9	11.1	d	e	1985, 1988, 1991–1993
Bełdany	941	46.0	10.0	d	e	1985, 1988, 1991, 1993–1995
Nidzkie	1818	23.7	6.2	d	m-e	1985, 1988, 1991–1995
Śniardwy	10970	23.4	5.8	p	e	1985, 1988, 1991–1995
Seksty	370	6.3	–	p	e	1985, 1988, 1991–1995
Łuknajno	680	3.0	0.6	p	m-e	1985, 1988, 1991–1995
Tyrkło	236	29.1	9.7	d	e	1991–1995
Tuchlin	219	4.9	2.8	p	e	1991–1995
Białoławki	211	36.1	9.8	d	m	1991–1995

Abbreviations: d – dimictic, p – polymictic, m – mesotrophic, m–e – mesoeutrophic, e – eutrophic, pt – polytrophic.

3. RESULTS

Twenty two taxa of submerged aquatic macrophytes (including free-floating plants) were found in the analysed littoral transects. Twelve out of 22 dominated in the total biomass over the whole sampling period. Occurrence of the dominating species was related to nutrient content in lake water. *Potamogeton pectinatus* L. tolerated TP concentrations from several μg P dm^{-3} to over 800 μg P dm^{-3}. *Myriophyllum spicatum* L. and *Fontinalis antipyretica* Hedw. showed also high tolerance to phosphorus concentrations in lake water (Fig. 1). Other representatives of the genus *Potamogeton* (*P. perfoliatus* L., *P. mucronatus* Schrad. and *P. lucens* L.) were found in waters with considerably lower TP concentrations, though the tolerance of two latter, due to their scarcity, can hardly be assessed.

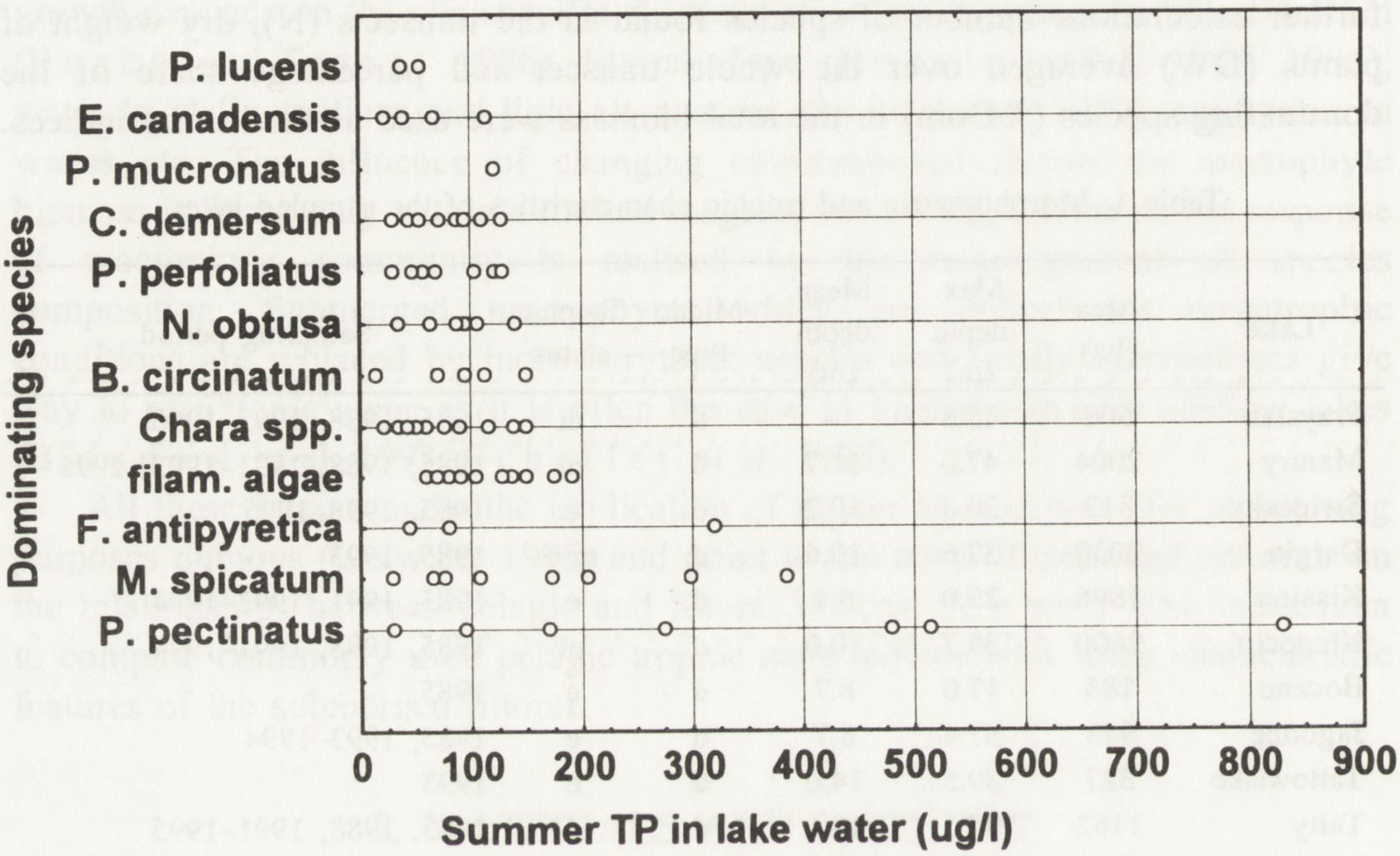

Fig. 1. Occurence of the dominating plant species in waters of different total phosphorus concentrations (each circle represents one sampling occasion)

Contrary to total P, dominating plant species were not so much diversified in their tolerance to total nitrogen (Fig. 2). Again *Potamogeton pectinatus* was present in waters of a wide range of TN concentrations, but *Myriophyllum spicatum*, filamentous algae, *Batrachium circinatum* Fr. and *Chara* spp. also tolerated waters with over 2.5 mg TN dm^{-3}.

The relationships between TP and SD visibility and TP and chlorophyll a for waters of the Great Masurian Lakes differed markedly from those derived by Carlson (1977). Chlorophyll concentrations and SD were, as a rule, lower than those one should expect from the total P levels – see Fig. 3 as an example. That is why, for further calculations we used the absolute nutrient concentrations instead of trophic state indices to characterise pelagic environment.

SD visibility correlated positively with maximum depth of plant occurrence and the total number of submerged plant species (Table 2). Also strong but negative correlation was found between these two littoral parameters and the concentration of chlorophyll a in lake water. Relationships between maximum depth and the number of species on one side and nutrient concentrations on the other, though significant, were weaker (Table 2). Water transparency did not affect the biomass of submerged plant species in the analysed transects, there was, however, negative relationship between the plant dry weight and chlorophyll concentration. Weak negative correlation was also found between dry weight of plants and TP and TN concentrations, the latter was statistically insignificant. Percentage biomass of dominating species and the

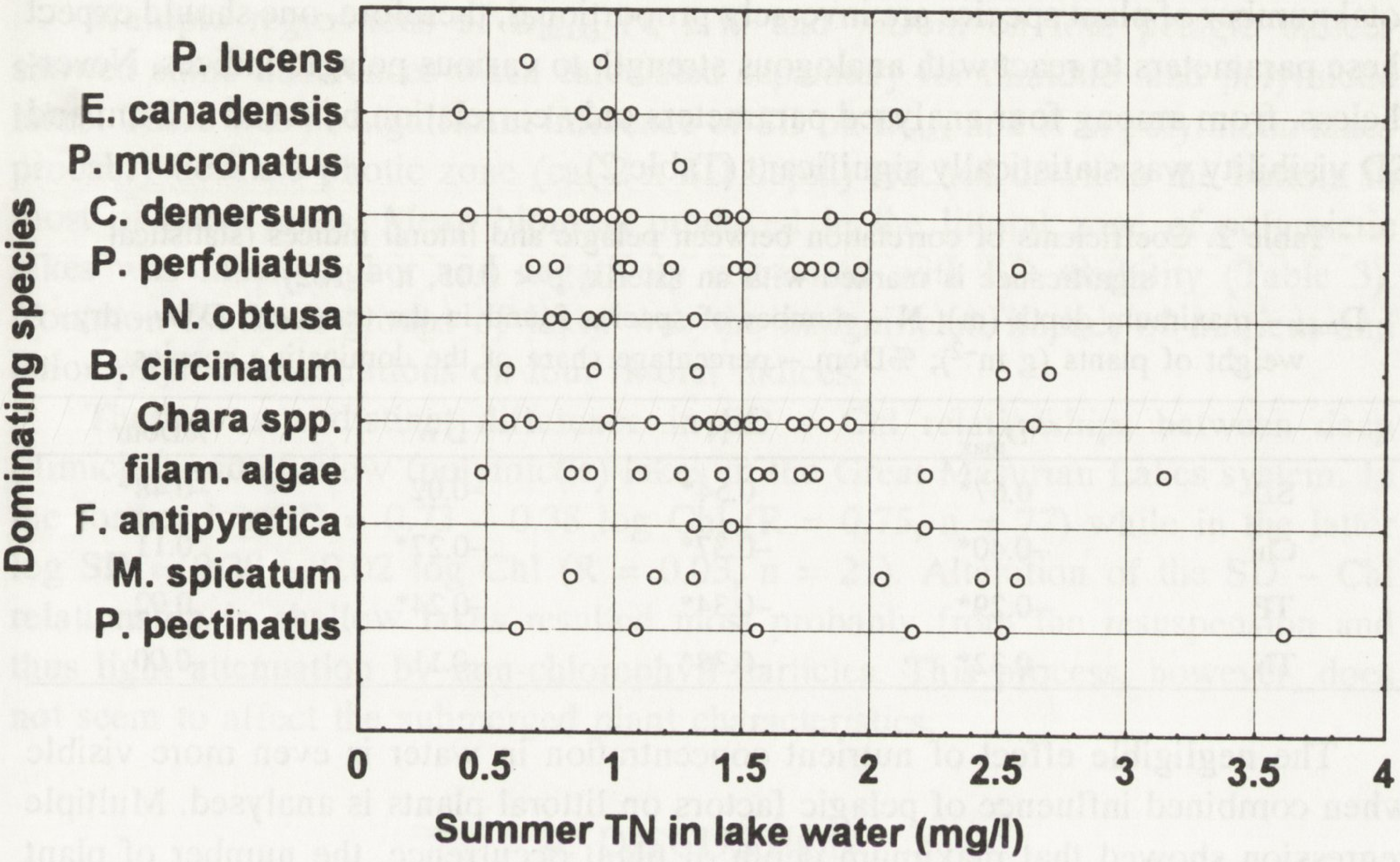

Fig.2. Occurence of the dominating plant species in waters of different total nitrogen concentrations (each circle represents one sampling occasion)

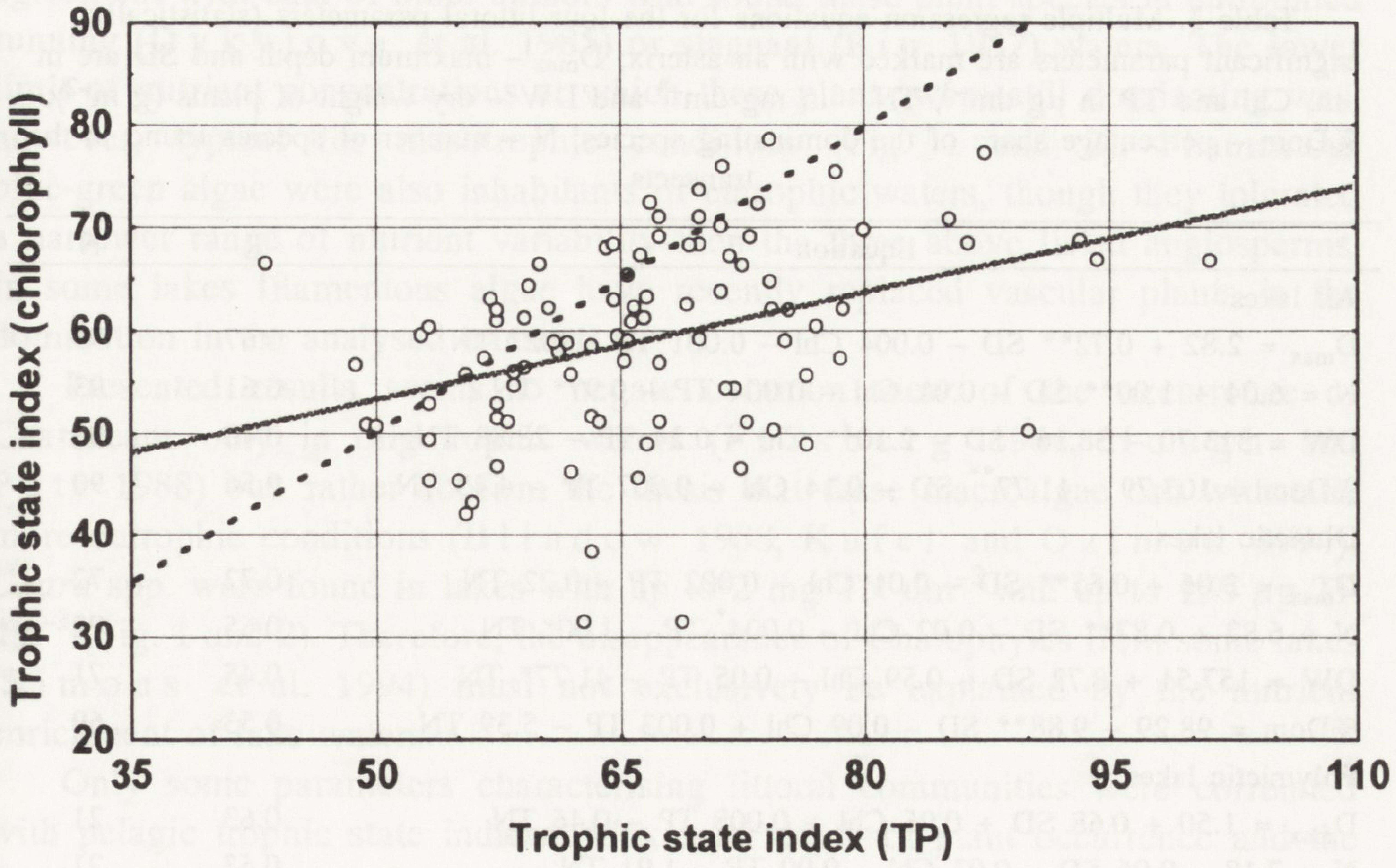

Fig. 3. Comparison of the trophic state indices calculated from chlorophyll and total phosphorus concentrations based on present results (solid line) and on Carlson's (1977) model (dotted line) (each circle represents one sampling occasion)

total number of plant species are inversely proportional, therefore, one should expect these parameters to react with analogous strength to various pelagic indices. Nevertheless, from among four analysed parameters only correlation between %Dom and SD visibility was statistically significant (Table 2).

Table 2. Coefficients of correlation between pelagic and littoral indices (statistical significance is marked with an asterix, $p < 0.05$, $n = 102$)
D_{max} – maximum depth (m); N – number of species found in the transects; DW – dry weight of plants ($g\ m^{-2}$); %Dom – percentage share of the dominating species

	D_{max}	N	DW	%Dom
SD	0.67*	0.54*	–0.02	–0.48*
Chl	–0.40*	–0.37*	–0.27*	0.11
TP	–0.29*	–0.34*	–0.24*	0.02
TN	–0.32*	–0.38*	–0.11	–0.00

The negligible effect of nutrient concentration in water is even more visible when combined influence of pelagic factors on littoral plants is analysed. Multiple regression showed that maximum depth of plant occurrence, the number of plant species, dry weight and the percentage biomass of dominating species depended only on SD visibility (Table 3) while TP and TN exerted insignificant influence on submerged littoral plants.

Table 3. Multiple regression equations for the four littoral parameters (statistically significant parameters are marked with an asterix; D_{max} – maximum depth and SD are in m, Chl and TP in $\mu g\ dm^{-3}$, TN – in $mg\ dm^{-3}$ and DW – dry weight of plants ($g\ m^{-2}$); %Dom – percentage share of the dominating species; N – number of species found in the transects

Equation	R	N
All lakes		
D_{max} = 2.82 + 0.72** SD – 0.004 Chl – 0.001 TP – 0.27 TN	0.67	93
N = 6.04 + 1.00** SD – 0.01 Chl – 0.004 TP – 0.97* TN	0.61	93
DW = 313.70 – 38.16* SD – 2.10** Chl – 0.24 TP – 28.88 TN	0.40	92
%Dom = 103.79 – 11.77** SD – 0.14 Chl – 0.007 TP – 4.43 TN	0.56	90
Dimictic lakes		
D_{max} = 3.06 + 0.65** SD – 0.01 Chl – 0.002 TP – 0.22 TN	0.72	72
N = 6.82 + 0.87** SD – 0.02 Chl – 0.004* TP – 1.00* TN	0.65	72
DW = 157.51 + 8.72 SD – 0.59 Chl – 0.05 TP – 41.77* TN	0.45	71
%Dom = 98.29 – 9.88** SD – 0.09 Chl + 0.003 TP – 5.39 TN	0.53	69
Polymictic lakes		
D_{max} = 1.50 + 0.68 SD + 0.05 Chl + 0.008 TP – 0.46 TN	0.63	21
N = 7.18 – 0.06 SD – 0.03 Chl – 0.00 TP – 1.91 TN	0.53	21
DW = 951.65 – 265.62** SD – 8.76 Chl – 1.94* TP – 16.87 TN	0.80	21
%Dom = 130.40 – 23.05** SD – 0.17 Chl – 0.10 TP – 4.09 TN	0.76	21

*$p < 0.05$, ** $p < 0.01$.

Multiple regressions of D_{max}, N, DW and %Dom on four pelagic indices showed some differences when calculated separately for dimictic and polymictic lakes. There was no significant influence of SD on D_{max} and N in polymictic lakes probably because photic zone (ca. 2 x SD depth) reached down to the bottom in most of these lakes. Mean biomass produced in the littoral zone of polymictic lakes was much higher and negatively correlated with SD visibility (Table 3). Common for both groups of lakes was the insignificant impact of nutrient and chlorophyll concentrations on four littoral indices.

There was a distinct difference in SD – Chl relationships between deep (dimictic) and shallow (polymictic) lakes in the Great Masurian Lakes system. In the former log SD = 0.73 – 0.38 log Chl (R = 0.75, n = 77) while in the latter log SD = 0.20 – 0.02 log Chl (R = 0.03, n = 21). Alteration of the SD – Chl relationship in shallow lakes resulted most probably from the resuspension and thus light attenuation by non-chlorophyll particles. This process, however, does not seem to affect the submerged plant characteristics.

4. DISCUSSION

The observed dominance of *Potamogeton pectinatus, P. perfoliatus* and *Myriophyllum spicatum* in waters with high N and P concentrations is in agreement with data of other authors who found these plant species in eutrophied running (Dykyjova et al. 1985) or stagnant (Pip 1987) waters. The lower limit of nutrient concentrations at which these plants were still dominating was, however, typical for mesotrophic conditions (Fig. 1 and 2). Filamentous blue-green algae were also inhabitants of eutrophic waters, though they tolerated a narrower range of nutrient variability then the three above listed angiosperms. In some lakes filamentous algae have recently replaced vascular plants in the domination in the analysed transects.

Presented results seems to negate common view of the occurrence of Characeans only in oligotrophic waters (Forsberg 1964, Hough and Putt 1988) but rather confirm the thesis that these macroalgae can withstand more eutrophic conditions (Blindow 1988, Kufel and Ozimek 1994). *Chara* spp. were found in lakes with up to 2 mg TN dm^{-3} and up to 150 μg TP dm^{-3} (Fig. 1 and 2). Therefore, the disappearance of Charophytes from some lakes (Simons et al. 1994) must not exclusively be explained by the nutrient enrichment of lake waters.

Only some parameters characterising littoral communities were correlated with pelagic trophic state indices. Maximum depth of plant occurrence and the number of species correlated with all pelagic indices (Table 2). The regression of D_{max} on Secchi disc depth (D_{max} = 1.94 + 0.88 SD, R = 0.67, n = 102) was close to that calculated by Duarte and Kalff (1990) for 25 Canadian and American lakes. Linear regression showed, however, lower than predicted D_{max}

for the extreme Secchi disc depths (Fig. 4) suggesting other than linear type of regression. Non-linear character of SD records in lake water was underlined in the critical comments by Lorenzen (1980) and Megard et al. (1980) to Carlson's (1977) model of SD-chlorophyll relationships. Reasons listed in these comments have particular significance for littoral zone and macrophytes. First to be mentioned is the variable effect of bottom resuspension which, at a given turbulence, delivers more sediment particles to water in shallow than in deeper sites of the littoral transect.

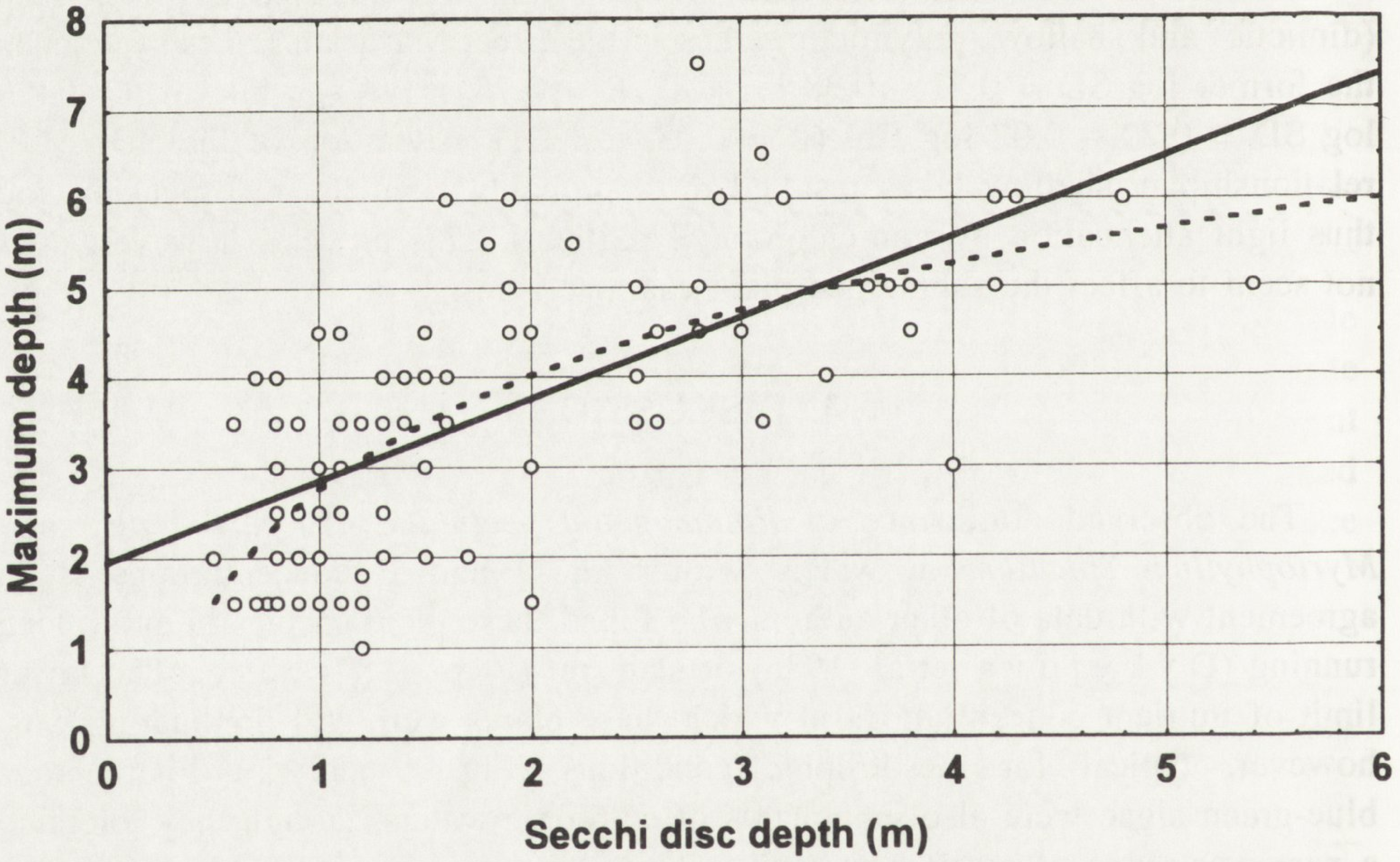

Fig. 4. Linear and logarithmic approximation of the maximum depth of plant occurrence plotted on Secchi disc visibility in pelagial zone (each circle represents one sampling occasion)

Therefore, local (littoral) water transparency could be lower (at least occasionally) than SD measured in the open water pelagic area. When phytolittoral is limited only to shallow parts of the lake (low SD visibility) D_{max} could be smaller than predicted from linear regression. Background attenuation and filtering properties of the water itself may determine the range of macrophyte colonisation in the opposite situation (high SD). Selective light penetration makes only part of visible irradiance (mostly green and orange) reach deeper zones of a lake. We do not have data on the macrophyte requirements for light of a definite wavelength, we can only hypothesise that maximum depth of plant occurrence can be limited in deep water by light which is visible but not photosynthetically available. That is why logarithm approximation (D_{max} = 2.78 + 4.14 log SD, R = 0.70, n = 102 – see Fig. 4) seems to be better than linear to describe the effect of water transparency on submerged macrophytes.

The regression of D_{max} on chlorophyll concentration was weaker though still statistically significant. We assume that chlorophyll influenced macrophytes indirectly, through shadowing rather than through other mechanisms (like phytoplankton competition for nutrients etc.). The dispersion of observed data around regression line ($D_{max} = 4.03 - 0.02$ Chl, R = 0.40, n = 103) was the largest in the region of low chlorophyll concentrations, probably due to the increasing share of non-chlorophyll suspended particles in the formation of the light regime in the littoral site.

Number of species was also strongly related to water transparency (Table 2). As for D_{max}, linear regression presented marked deviations from linearity, especially for minimum SD values. Thus, we suggest logarithm regression (N = 4.77 + 6.46 log SD, R = 0.56, n = 102) which, except slightly better approximation, gives reasonably N = 0 for SD = 0.18 m while at the same transparency linear model (N = 3.43 + 1.39 SD, R = 0.54, n = 102) gives N = 3.8. It is not clear, however, whether light climate enhances species diversity directly or it was rather an indirect effect of the general trophic status of lake waters.

The response of submerged plant biomass to increased nutrient concentrations is a matter of discussion in the literature. Extremely high nutrient concentrations (e.g. near sewage outlets) eliminate most of aquatic macrophytes (Ozimek 1978) while, within a certain range of nutrient level, various submerged plant species (Anderson and Kalff 1986, Kufel and Ozimek 1994) can be nutrient limited. Chambers and Prepas (1990), on the contrary, presented evidence for the lack of nitrogen and phosphorus impact on the biomass of *Myriophyllum exalbescens, Ceratophyllum demersum* and *Chara* spp. Our results seem to confirm the latter findings. Mean dry weight of plants and the percentage share of dominating species in the total plant biomass showed the weakest relationships to abiotic factors (except for shallow lakes – Table 3). Low statistical significance of the regressions resulted probably from varying species composition of submerged littoral and replacement of one species by the others, each of different specific biomass and density. In fact, only in four lakes the same plant species dominated in biomass during the period under study. In other lakes a shift in species composition was observed. In meso- or mesoeutrophic lakes Charophytes were usually replaced by *Elodea canadensis* Rich., plants of the genus *Potamogeton* or filamentous blue-green algae. In eutrophic lakes there was no regular tendency and the dominance in biomass happened to change from year to year. Respective regression equations did not change significantly even when calculated only for those cases where the dominating plant species were *Chara spp., Nitellopsis obtusa* (Desvaux) or filamentous algae i.e. those plants, which are, more than rooted angiosperms, subjected to nutrient content in the ambient waters.

There was also no significant relationship between nutrient concentrations in water and DW or %Dom calculated for only one dominating species. Remarkably, all regression coefficients for nutrient concentrations, though insignificant at

$p < 0.05$, were negative. It may suggest indirect impact of nutrients on plant biomass through the increased phytoplankton production and thus light attenuation in the investigated littoral stands.

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5. SUMMARY

A comparison has been made between pelagic trophic state indices (SD depth, chlorophyll *a* concentration and concentrations of total P and total N) and parameters that characterise macrophyte communities in the littoral zone (maximum depth of plant colonisation, number of species, mean plant biomass and % share of the dominant species in the total biomass). The data are from 20 lakes in the Great Masurian Lakes system (north-eastern Poland) and were collected between 1985 and 1995.

Twelve out of 22 found plant species were dominating in the analysed littoral transects. Plants presented distinct differences in their tolerance to TP concentration in lake water. ***Potamogeton pectinatus*, *Myriophyllum spicatum*** and ***Fontinalis antipyretica*** dominated in stands with a wide range of TP concentration in water (up to 830 $\mu g\ P\ dm^{-3}$) while the dominance of ***P. perfoliatus*, *P. lucens*, *P. mucronatus*** and ***Elodea canadensis*** was restricted to waters with much lower TP concentrations (Fig. 1). Tolerance of the same species to TN in lake water was not so distinctly different (Fig. 2).

Maximum depth of plant colonisation and the number of species correlated with all pelagic indices, the most significant impact being exerted by SD visibility (Table 2). Plant biomass and % of the dominant in the total biomass of macrophytes were poorly related to water transparency and nutrient status of pelagic waters (Table 2) probably due to the replacement of one dominating species by the other, each of different specific biomass and density. Similar lack of nutrient influence on littoral indices can be seen from multiple regression equations calculated for each of littoral factors on the four pelagic indices (Table 3). When calculated separately for di- and polymictic lakes, regression equations did not show the influence of water transparency (expressed either by SD or by chlorophyll content) on D_{max} and N in shallow lakes, probably due to the extension of photic zone to the bottom.

To sum up, the best predictors of the trophic status of a lake seem to be maximum depth of macrophyte occurrence and the number of species in the littoral zone. Biomass of macrophytes was poorly related to pelagic indices and nutrient concentrations affected littoral structure to a minor extent.

6. POLISH SUMMARY

Porównano pelagiczne wskaźniki stanu trofii (widzialność krążka Secchiego, stężenie chlorofilu, azotu i fosforu całkowitego) z parametrami charakteryzującymi zespoły makrofitów w strefie litoralnej (maksymalna głębokość występowania, liczba gatunków, średnia biomasa makrofitów i procentowy udział dominanta w ogólnej biomasie makrofitów). Dane pochodzą z 20 jezior systemu Wielkich Jezior Mazurskich i były gromadzone w latach 1985–1995.

Spośród 22 taksonów makrofitów 12 dominowało w biomasie w analizowanych transektach strefy litoralnej. Rośliny wykazywały różną tolerancję na stężenie całkowitego fosforu w wodzie jeziornej. *Potamogeton pectinatus*, *Myriophyllum spicatum* i *Fontinalis* *antipyretica* dominowały w stanowiskach, w których stężenie fosforu zmieniało się w szerokich granicach (do 830 μg P dm^{-3}) podczas gdy dominacja *P. perfoliatus*, *P. lucens*, *P. mucronatus* i *Elodea canadensis* ograniczona była do stanowisk o mniejszym przedziale zmian TP (rys. 1).

Dominujące gatunki nie były tak wyraźnie zróżnicowane wobec zmienności stężeń całkowitego azotu w wodzie jeziornej (rys. 2).

Stwierdzono istotną korelację między maksymalną głębokością występowania roślin i liczbą gatunków a czterema pelagicznymi wskaźnikami trofii, z których najsilniejsze oddziaływanie wykazywała widzialność krążka Secchiego (tab. 2). Biomasa roślin i procentowy udział dominanta w ogólnej biomasie były słabo uzależnione od przezroczystości wody i poziomu pierwiastków biofilnych w wodach pelagialu (tab. 2) prawdopodobnie z powodu wypierania jednych gatunków makrofitów przez inne, o różnej biomasie i gęstości. Podobny brak wpływu pierwiastków biofilnych na wskaźniki litoralne przedstawiają równania regresji wielokrotnej (tab. 3). Analogiczne równania obliczone oddzielnie dla płytkich jezior polimiktycznych wykazały brak wpływu przezroczystości wody (wyrażonego przez SD lub przez zawartość chlorofilu) na zasięg występowania i liczbę gatunków makrofitów, powodem był tu zasięg strefy fotycznej, w większości płytkich jezior pokrywający się z głębokością.

Podsumowując, należy stwierdzić, że maksymalny zasięg występowania makrofitów i liczba gatunków w litoralu są dobrymi wskaźnikami stanu trofii. Biomasa makrofitów jest słabo uzależniona od pelagicznych wskaźników trofii a poziom azotu i fosforu w wodzie w niewielkim stopniu oddziaływuje na strukturę roślinności strefy litoralnej.

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