RESPONSE OF HORNWORT (*CERATOPHYLLUM DEMERSUM* L.) TO WATER LEVEL DRAWDOWN IN A TURBID WATER RESERVOIR

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Abstract. The research focuses on the effects of seasonal water level drawdown on the submerged vegetation in a turbid water reservoir measured through the biomass, the maximum depth of colonization and the occurrence frequency of hornwort *Ceratophyllum demersum* L. Furthermore, the underwater light intensity, water turbidity and biovolume of planktonic algae were determined to evaluate the environmental factors affecting the development of macrophytes. Because of low global radiation in late summer, the irradiance in the period following the water level drawdown was lower compared to the preceding period, but still above the species tolerance level. Nonetheless, the water level regulation improved the underwater light conditions for submerged macrophytes through the water level reduction. Plant biomass, the incidence of *C. demersum* and the maximum depth of macrophyte colonization increased after the water level drawdown in deep phytolittoral, whereas no effects were observed in shallows. Our research showed that the water level changes could be a useful tool in treatments aimed at maintaining the aquatic vegetation and improving the water quality in regulated water bodies.
Keywords: *macrophytes, phytolittoral, water level drawdown, hornwort*

Introduction

Submersed macrophytes play a key role in freshwater shallow ecosystems. They provide habitats and refuges for predatory fish and zooplankton, which may indirectly inhibit phytoplankton abundance (Jepessen et al., 1998). Macrophytes reduce the resuspension processes and increase the sedimentation rate, which improves the water transparency (Madsen et al, 2001; Søndergaard et al., 2003). Some macrophyte species may inhibit the growth of algae by effective competition for nutrients and allelopathic activity (Scheffer et al., 1993; Nakai et al., 1999). Hence, changes in macrophyte biomass are likely to have an important effect on the lake ecosystem.

Hornwort *Ceratophyllum demersum* L. may play an important structuring role in eutrophic lakes and reservoirs. It is a submerged, perennial plant with no roots, which often grows with the base of the stem buried in sediments, attached to the lake bottom by modified leaves. Hornwort can hamper the phytoplankton growth in shallow eutrophic lakes, which contributes to the stabilization of the macrophyte-dominated state characterized by clear water (Gross et al., 1993; Mjelde and Faafeng, 1997). The species is very common in turbid, disturbed shallow water bodies, such as man-made reservoirs, due to its high tolerance to shade and disturbance (Ali et al., 1995, 2011).

A specific, annual water-level cycle in man-made reservoirs is related to water management for hydropower, agricultural use, fishery, flood prevention or recreation

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(Geraldes et al., 2005). This contributes to an increase in the annual and inter-annual amplitude of the water level fluctuations, which are usually much higher than in natural lakes affected only by climatic and hydrological factors (Noges et al., 2003; Haldna et al., 2008). Changes in the water level strongly affect the aquatic vegetation abundance in water bodies (Hellsten, 2002; Coops et al., 2008). A relatively large number of studies dealt with effects of annual water-level fluctuations on macrophytes, however data on the role of intra-annual variability are scanty and limited to subtropical freshwaters (Thomaz et al., 2006).

Shallow man-made reservoirs may undergo rapid eutrophication due to the nutrient load from rivers and canals (Solis et al., 2012). High water turbidity related to over-fertilization and high algal biomass causes deterioration of the underwater light climate, thus affecting the structure and abundance of macrophytes in such disturbed lakes (Scheffer et al., 1993).

It seems, however, that the water level drawdown can stimulate the re-development of submerged macrophytes (Beklioglu et al., 2006; Bucak et al., 2012), thus making such operations a potentially useful tool in restoration of reservoirs. The aim of the study was to investigate the effect of water level drawdown in a shallow, turbid water reservoir on short-term dynamics of hornwort (*C. demersum*). Additionally, we aimed at evaluating the effect of light conditions on the plant biomass after the water level lowering.

Material and methods

Lake Domaszne (51°28’14” N, 23°00’07” E) is a small (95 ha), shallow (max. depth 3.1 m) and polymictic reservoir situated in the West Polesie region in Eastern Poland. The reservoir originates from natural Lake Domaszne, which was embanked and included in the hydrological system of the Wieprz-Krzna Canal. The water level in the reservoir is regulated to ensure the water supply for irrigation management and fish farming. Nutrient-rich water from the canal contributed the most to the present eutrophic/hypertrophic conditions of the water body (Solis, 2012).

Based on the data obtained from the local water management authorities, the water level in Lake Domaszne fluctuated in the hydrological year of 2007. The reservoir was filled up with water from the Canal in November-December 2006, and then again in April 2007 in order to replenish the water resources before the summer season. Water from the reservoir was discharged twice: in March and in June-July 2007. Thus, the study season 2007 was divided into two periods in terms of water level fluctuations and hydrological stages: the first one between the 1st of April and the 12th of July and the second one between the 12th of July and the 30th of September, hereafter referred to as the “early period” and the “late period”, respectively (*Fig. 1*). Based on the data from the watermark, the mean water level in the successive periods was on average of 2.56 and 2.06 m, respectively. The mean volume of the reservoir changed from 1.98 10^6 m^3 to 1.52 10^6 m^3, respectively.

The macrophyte community was studied in a monospecific bed of *Ceratophyllum demersum* situated in large shallows (ca. 0.2 km^2) in the northern part of the reservoir. Hornwort samples were collected on the 12th of July and the 30th of September 2007 with a rake sampler from 0.4×0.4 quadrates. A total of 160 samples were collected randomly at two locations: in the shallow phytolittoral (Zone I, depth of 1.1-1.3 m) and in the deep phytolittoral (Zone II, depth of 1.5-1.8 m). Based on sampling depths, the

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sampling isobaths were calculated and they were expressed in terms of elevation above watermark zero (150.31 m a.s.l.). Plant samples were collected in September from the same isobaths as in July, regardless of the current water level. After sampling, plants were cleaned, dried at a temperature of 105 ºC to constant weight and then weighed.

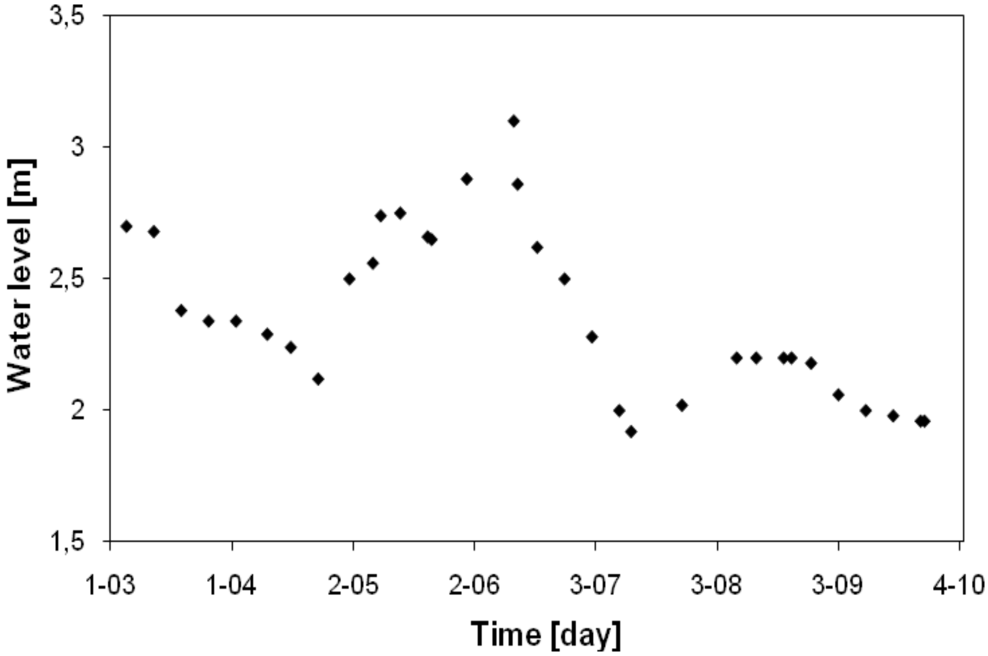

Figure 1. *Relative water levels in Lake Domaszne based on the watermark readings in 2007. Arrows indicate sampling dates.*

The maximum depth of macrophyte colonization (Z_c) was determined on the same dates at additional 70 sites.

Water transparency was considered as an attenuation coefficient, calculated from the measurements of PAR performed in situ using a Li-Cor meter (Li-250A) with an underwater quantum sensor (Li-192SA). The mean PAR above the bottom was calculated according to the following formula (Behrendt and Nixdorf, 1993):

$$I_{PAR} = 0.45\ I_0 \left(\frac{1-e^{-K_d Z_b}}{K_d\ Z_b}\right) \quad \text{(Eq.1)},$$

where Z_b is a water depth, K_d is an attenuation coefficient (m^{-1}) and I_0 is an average daily global radiation (J cm^{-2} d^{-1}). The contribution of PAR was calculated by a correction factor of 0.45 (Eq. 1). Data on global radiation were obtained from the meteorological station in Włodawa situated ca. 40 km from the reservoir.

Phytoplankton was sampled every two weeks between April and September. The abundance was estimated after fixation with Lugol's solution in sediment chambers according to Wetzel and Likens (2000). Biovolume was calculated using the geometric formulas after prior measurements of corresponding dimensions (Hillebrand et al., 1999).

The data were log-transformed prior to statistical analysis or non-parametric tests were used if data did not meet assumptions of parametric tests. The effects of the water level drawdown on the plant biomass was analysed by two-way ANOVA. The normality of the

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data was tested by the Lilleforst test and the homogeneity of variance was tested by the Levene test. Post-hoc Tukey's test was used to compare particular groups in ANOVA. Other differences were analysed by the Mann-Whitney test. The relationship between water transparency and phytoplankton was evaluated by Spearman's rank correlation test. All calculations were performed with Statistica 9.1 software (Sokal and Rohlf, 1995).

Results

The abundance of *Ceratophyllum demersum* in Lake Domaszne was significantly correlated with the depth of phytolittoral in terms of elevation above zero of the watermark, irrespective of the water level fluctuations (*Table 1*). Dry biomass was on average 151.6 g m^{-2} in the shallow phytolittoral (Zone I) and 21.4 g m^{-2} in the deep phytolittoral (Zone II).

Table 1. *Effects of location in phytolittoral (Zone), water level (Drawdown) and their interaction (Drawdown × Zone) on dry mass of Ceratophyllum demersum in the regulated lake; df – degrees of freedom, F – F-test, p – significance level*

Effect	df	F	p
Zone	1	212.58	<0.001
Drawdown	1	0.42	>0.5
Drawdown × Zone	1	12.31	<0.001

As expressed by the significance of Drawdown × Zone interaction, the response of *C. demersum* to drawdown was significant, with different effects on the biomass both in the shallow and deep phytolittoral (*Table 1*). The biomass in Zone I declined by 22%, however, the effect was not significant (Tukey's test, $p > 0.5$) (*Fig. 2*).

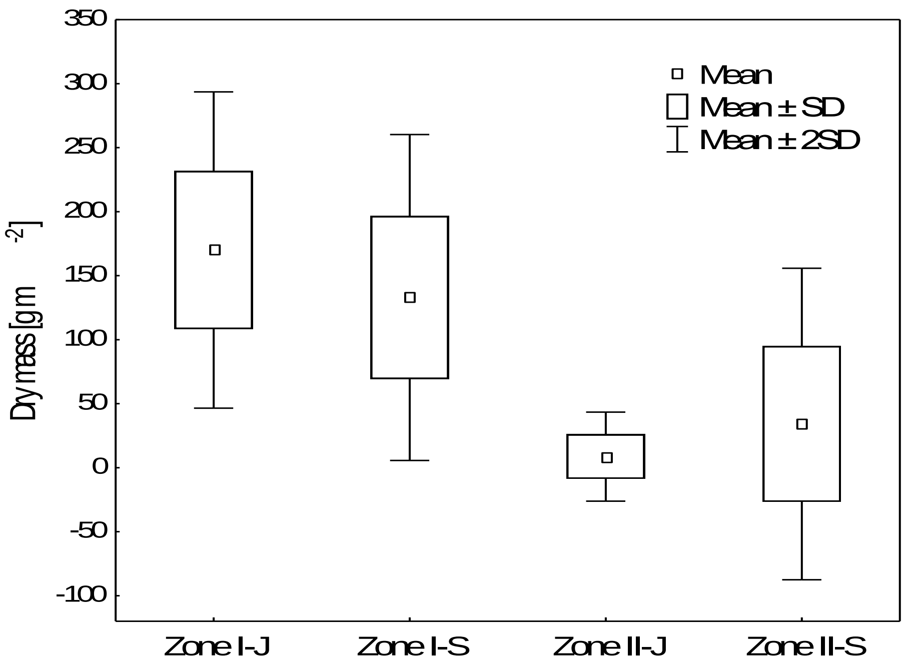

Figure 2. *Biomass of C. demersum in Lake Domaszne after water level drawdown at different depths; Zone I – shallow phytolittoral, Zone II – deep phytolittoral, E – early period, L – late period*

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The impact of the water level lowering on *C. demersum* was strongly significant in Zone II (Tukey's test, $p < 0.001$), where the biomass increased from 8.6 g m^{-2} in the early period to 34.2 g m^{-2} in the late period (*Fig. 2*).

Following the increased biomass, the frequency of *C. demersum* occurrence slightly increased after water level drawdown, i.e. from 45% (the early period) to 55% (the late period) in Zone II, whereas it was constant in Zone I (100% in both periods).

The maximum depth of macrophyte colonization (Z_c) reflected strong light limitation. The depth Z_c, measured in relation to the watermark zero, slightly but significantly decreased from 0.93 m in the early period to 0.87 m in the late period (U-test, Z = 2.72, $p < 0.01$). The depth in relation to water surface was on average 1.26 m (max. 1.7 m) in the early period and 1.23 m (max. 1.4 m) in the late period. The results indicate that *C. demersum* occurred in both periods nearly at the same depth, but it shifted to deeper isobaths not colonized before water drawdown.

The positive response of the submerged vegetation occurred despite the high water turbidity related to high algal abundance. Phytoplankton biovolume ranged from 11.7 mm^3 dm^{-3} in June to 29.2 mm^3 dm^{-3} in July (*Fig. 3*). The abundant occurrence of *Limnothrix redekei* (van Goor) Meff. and *Planktothrix agardhii* (Gom.) Anag. et Kom. was observed; on average the two species accounted for 38% and 24% of the phytoplankton biovolume, respectively. The accompanying taxa included other Cyanoprokaryota: *Limnothrix planctonica* (Wołosz.) Meff., *Aphanizomenon gracile* (Lemm.) Lemm., *Microcystis* spp. and *Chroococcus* spp. Apart from blue-greens, diatoms and chlorophytes contributed the most to the total phytoplankton biovolume. The water level drawdown did not significantly affect the amount of phytoplankton. No differences were found between the early and the late period, neither in total phytoplankton (U-test, Z =-0.82, $p > 0.05$) nor in Cyanoprokaryota biovolume (U-test, Z =-0.64, $p > 0.05$).

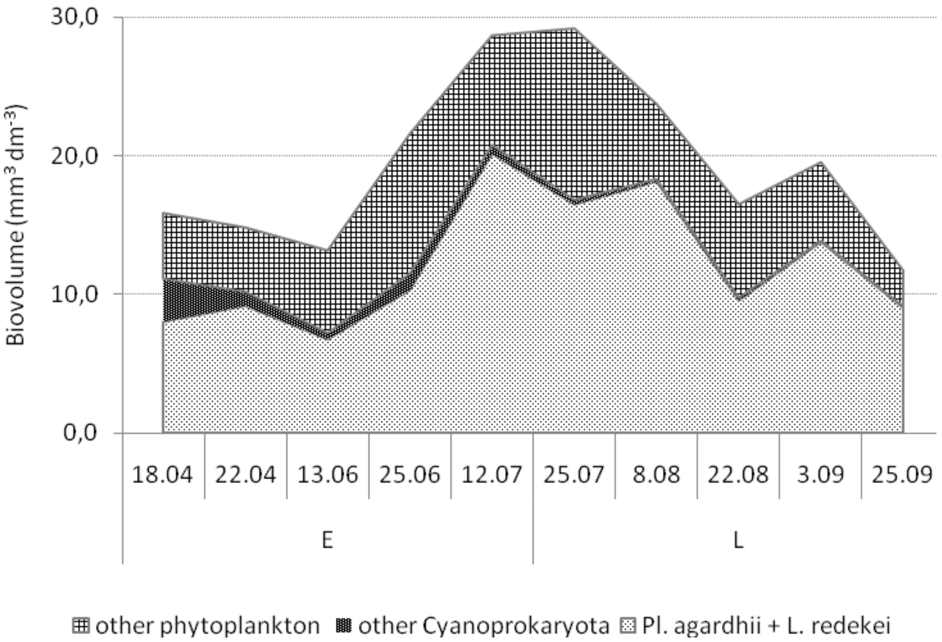

Figure 3. *Total phytoplankton biovolume in Lake Domaszne from April to September 2007; E – early period, L – late period*

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Water transparency in Lake Domaszne was similar in both periods (U-test, Z =-1.55, $p > 0.05$), while the attenuation coefficient (K_d) was 3.0 and 3.8 in the early and late period, respectively. Water turbidity was significantly correlated with the biovolume of phytoplankton (Spearman's test, R = 0.92, $p < 0.05$), especially the growth of blue-green algae (Spearman's test, R = 0.87, $p < 0.05$). It means that the growth of the latter affected the light conditions under the water surface in both periods.

The effects on *C. demersum* were observed despite the fact that light conditions were generally less favourable in the late period compared to the early one. Subsurface underwater PAR intensity (mean I_0) was 39.8 E m^{-2} d^{-1} in the early period and 27.4 E m^{-2} d^{-1} in the late period. A decrease in the light intensity above the bottom in deep phytolittoral ranged from 0.8 to 0.5 E m^{-2} d^{-1} for the early and late period, respectively. In the shallow phytolittoral it ranged from 1.3 to 1.1 E m^{-2} d^{-1}, respectively (*Fig. 4*). However, in terms of average percentage values of subsurface light, the irradiance at the bottom in Zone II was comparable in the early (2%) and in the late period (2.3%). Subsurface light intensity at the bottom in Zone I declined between the early and late period from 5.6% to 4.3%.

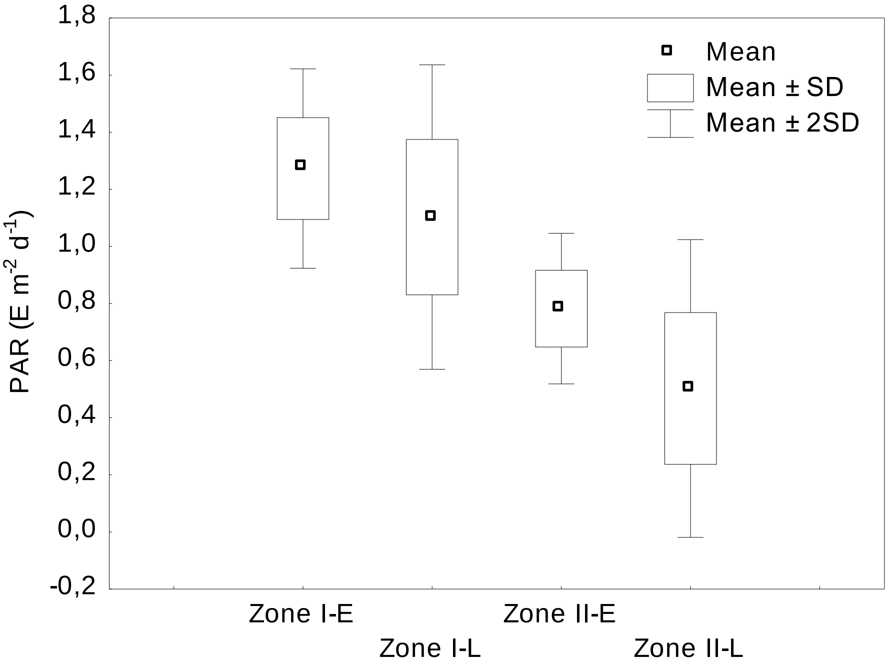

Figure 4. *Light intensity after water level drawdown in Lake Domaszne at different depths; Zone I – shallow phytolittoral, Zone II – deep phytolittoral, E – early period, L – late period*

Discussion

Water level fluctuations in shallow water bodies can affect the composition, diversity and abundance of macrophytes (Hellsten, 2002; Riis and Hawes, 2002). The effect of the water level changes on the submerged vegetation is, however, not straightforward. Several studies showed that a low water level during a vegetation season has a positive effect on submerged plant biomass (Blindow, 1992; Beklioglu et al., 2006; Bucak et al., 2012). On the other hand, macrophytes could be negatively affected by increased water turbidity after the water level lowering. Then, the increased resuspension caused by the

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wave action could cause a deterioration of water transparency and light conditions (Pieczyńska, 2008).

Extreme water drawdown in regulated lakes may be catastrophic for submerged macrophytes due to freezing-up of the exposed parts of the bottom in winter or their desiccation in summer. Thus, the water level manipulation may be used as a measure to control nuisance macrophytes in reservoirs (Rørslett and Johansen, 1996).

Submerged macrophytes in temperate lakes begin to senesce and die after reproduction in summer (Westlake, 1965). During the seasonal life cycle, the biomass of *Ceratophyllum demersum* declines from the seasonal maximum in June-July to the minimum in September or October (Asaeda and Bon, 1997; Nikolić et al., 2007) due to decreasing solar radiation and low temperatures (Wetzel, 2001). Contrary to previous studies from natural lakes, our research showed, that, the abundance of *C. demersum* in regulated Lake Domaszne tends to increase in late summer after the water level drawdown.

The effect of water level drawdown on *Ceratophyllum demersum* was correlated with the location in phytolittoral, similarly to a sub-tropical reservoir described by Thomaz et al. (2006). Plant biomass of *C. demersum* slightly decreased at shallow sites most likely because of self-shading, which is an important regulating mechanism of production and biomass growth in aquatic macrophytes (Westlake, 1965; Calado and Duarte, 2000). After the water level and the reservoir volume decreased the biomass of *C. demersum* in the shallow phytolittoral became more concentrated. The increased shoot density reduced the light in the macrophyte beds especially at shallow sites where *C. demersum* was very abundant. Organic matter deposited on plant organs (because of the increased sedimentation rate in dense macrophyte beds) could also negatively affect the vegetative growth of the submerged plants (Barko and Smart, 1986). Desiccation of the lake bottom after the water level drawdown was rather of little importance in the reservoir due to the shoreline regulation and inclination of lake shores.

In contrast to shallow phytolittoral, the biomass of *C. demersum* increased after the drawdown in deep phytolittoral and the vegetation shifted to a deeper, previously non-colonized area of the reservoir. As a consequence of the water level lowering, larger parts of the bottom have became exposed to more favourable light intensity in the water column, which affects the spread of *C. demersum* in late summer.

The effect of annual water level regime on the submerged macrophyte was observed despite the light conditions – in the late summer they were generally worse than during the preceding period. The shade tolerance of *C. demersum* seems to be the major factor responsible for the species relatively high abundance and common occurrence in turbid waters (Ali et al., 1995, 2011). Submersed macrophytes need, however, approximately 1-3% of the full sunlight spectrum (Wetzel, 2001). Hornwort could benefit from the water level regulation in the reservoir because light intensity in the water column was still above the species tolerance level and comparable to the light compensation point of the species (Van Nes et al., 2007).

Phytoplankton abundance is the major factor limiting the development of submerged macrophytes (Scheffer et al., 1993; Asaeda and Bon, 1997). Shallow reservoirs can be devoid of macrophytes due to a large amount of algae (Van Nes et al., 2007). High biomass of cyanobacteria caused high water turbidity and negatively affected the distribution of submerged vegetation in the lake (Scheffer and Van Nes 2007). On the other hand, sediment resuspension in shallow lakes can also affect the water turbidity (Jackson, 2003).

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The phytoplankton community in the studied reservoir was dominated by filamentous blue-green algae *Planktothrix agardhii* and *Limnothrix redekei*. Their abundant occurrence was observed mostly in shallow, polymictic and nutrient-rich water bodies, sometimes throughout the year (Solis et al., 2009; Kokociński et al., 2010). Both taxa are water-mixing and shade tolerant. According to Scheffer and Van Nes (2007), the presence of cyanobacteria from the Oscillatoria group can negatively affect the light conditions.

An increased abundance of submerged macrophytes affects the lake functioning and improves the water transparency, e.g. by negative effects on phytoplankton, increased sedimentation and by reduction of the resuspension rate (Scheffer et al., 1993; Horppila and Nurminen, 1997; Mjelde and Faafeng, 1997; Pęczuła et al., 2012). Moreover, the development of macrophyte beds stimulates other food-web components such as zooplankton and predatory fish, which are important for stabilization of clear-water conditions in a lake (Jeppesen et al., 1998). Several studies (e.g. Blindow, 1992; Bucak et al., 2012) highlighted the impact of inter-annual fluctuations in the water level on submerged macrophytes in shallow lakes as a shift between two alternative states: the vegetation-dominated one with clear-water conditions and the phytoplankton-dominated one with turbid water (Scheffer et al., 1993).

In conclusion, water level regulation within the annual cycle can improve the conditions for *C. demersum* development in a shallow, turbid water reservoir. Hence, it could be a helpful tool in treatments aimed at maintaining the aquatic vegetation and improving the water quality in such water bodies.

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