The effect of ice phenology exerted on submerged macrophytes through physicochemical parameters and the phytoplankton abundance

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ABSTRACT

*The physicochemical parameters of water, the concentration of chlorophyll-a and the submerged aquatic vegetation (SAV) were studied to evaluate the effects of different winter seasons on the biomass of macrophytes in shallow eutrophic lakes. We hypothesised that a lack of ice cover or early ice-out can influence the physicochemical parameters of water and thus change the conditions for the development of phytoplankton and SAV. The studies were conducted in four lakes of the Western Polesie region in mid-eastern Poland after mild winters with early ice-out (MW, 2011 and 2014) and after cold winters with late ice-out (CW, 2010, 2012 and 2013). The concentrations of soluble and total nitrogen, chlorophyll-a and the TN:TP ratio in the lakes were considerably higher, whereas the concentration of soluble and total phosphorus and water transparency were significantly lower after the MW compared with after the CW. No differences were found in water temperature, reaction and electrolytic conductivity. Low water turbidity linked with low concentration of chlorophyll-a after the CW resulted in increased water transparency and the total biomass of the SAV. The negative effect of the MW on the macrophyte species was stronger on more sensitive species (*Myriophyllum spicatum, Stratiotes aloides*) compared with shade tolerant* Ceratophyllum demersum. *Our findings show that the ice cover phenology affected by climate warming can change the balance between phytoplankton and benthic vegetation in shallow eutrophic lakes, acting as a shift between clear and turbid water states. We speculate that various responses of macrophyte species to changes in the water quality after two winter seasons (CW and MW) could cause alterations in the vegetation biomass, particularly the expansion of shade tolerance and the decline of light-demanding species after a series of mild winters.*

Key words: Aquatic vegetation; chlorophyll-a; ice cover; mild and cold winter; climatic effects; eutrophic lakes.

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INTRODUCTION

The current climate warming directly affects the temperature of surface water in lakes and indirectly physicochemical and biological processes related to temperature (Dokulil, 2014). A strong effect of the climate change is observed in winter, when varied meteorological conditions influence the phenology of ice cover on lakes. Mild winters, which are characterised by relatively high mean air temperatures and a short period of ice cover on lakes, are a product of the current climate change. A positive trend in annual air temperature in the Northern Hemisphere causes late ice formation and early ice cover thawing (Magnuson *et al.*, 2000; Livingstone *et al.*, 2010; Peng *et al.*, 2013). The duration of ice cover is non-linearly correlated with air temperature; thus, the trend towards earlier ice break-up is generally stronger in lower than higher latitudes (Weyhenmeyer *et al.*, 2004, 2005). This effect is even stronger in Central Europe (including Poland) compared with Northern Europe. In different regions of Poland, the mean air temperature in some winter and spring months (February, March and May) has increased over the last few decades (Degirmendžić *et al.*, 2004; Kaszewski *et al.*, 2009). In the Polish lowland lakes, this trend causes longer periods of

ice-free conditions and much earlier dates of the latest ice break-up − on average, from 0.6 to 0.8 days per year (Marszelewski and Skowron, 2006).

The ice cover influences the environmental conditions in water and the ecological functioning of lakes. It stabilises thermal conditions in water bodies and affects the underwater light climate and water chemistry (*e.g.*, nutrients and dissolved organic carbon concentration), the occurrence of winter fish kill and the production and diversity of phytoplankton and zooplankton (Ohlendorf *et al.*, 2000; Hargeby *et al.*, 2004; Christoffersen *et al.*, 2008; Ejankowski and Lenard, 2015). The increased mixing during ice-free winters can facilitate the alteration of the ecological status of the lake (Livingstone *et al.*, 2010). After mild winters, the nutrient concentration, phytoplankton biomass, water turbidity and temperature are generally higher than after cold winters (Gerten and Adrian, 2000; Weyhenmeyer *et al.*, 2008; Lenard and Wojciechowska, 2013). The earlier thawing of snow and ice can result in the earlier occurrence of the phytoplankton spring bloom (Weyhenmeyer *et al.*, 1999; Laugaste *et al.*, 2010), which determines the light climate for the growth of macrophytes (Blindow, 1992; Asaeda and Bon, 1997).

The influence of ice phenology on physicochemical parameters and phytoplankton productivity in these waters suggests that there is also a relationship between the duration of ice cover and the abundance of submerged aquatic macrophytes. The expected effect could be restricted to a rather short post-winter period after ice break-up (Gerten and Adrian, 2000; Weyhenmeyer *et al.*, 2008). The early ice thawing could decrease the vegetation biomass as a consequence of increased turbidity and restricted light penetration in the water column. Thus, it could change the balance between phytoplankton and vegetation in shallow eutrophic lakes, as a shift between clear and turbid water states (Wallsten and Forsgren, 1989; Scheffer and van Nes, 2007). However, this effect could be negligible because in temperate lakes, the productivity and biomass of macrophytes considerably increase during the growing season together with light and temperature conditions, reaching the maximum in summer (Westlake, 1965; Asaeda and Bon, 1997; Nikolić *et al.*, 2007).

The concentrations of mineral forms of nutrients, such as, ammonia and nitrate nitrogen or phosphate phosphorus, in lakes are often higher after a mild winter (Weyhenmeyer *et al.*, 2008; Laugaste *et al.*, 2010; Pełechata *et al.*, 2015), which may be related to permanent water mixing during ice-free winters (Lenard and Wojciechowska, 2013). Thus, a larger portion of soluble nutrients may be available for primary producers in the following season and can lead to phytoplankton blooms (Uchmański and Szeligiewicz, 1988). Furthermore, the occurrence of high phytoplankton biomass coupled with high water turbidity after a mild winter may delay the onset of the stratification period (Gerten and Adrian, 2001), which can influence future phytoplankton composition. If the effect of the absence of ice cover on lakes is extended over time, the biomass of many macrophyte populations will be negatively affected during the summer season (Netten *et al.*, 2011). However, this effect can be reversed in lakes with overwintering charophyte meadows, which are able to maintain high water clarity by limiting the development of phytoplankton (Pełechata *et al.*, 2015).

Macrophytes play an important role in the ecological functioning of lakes and reservoirs. They provide habitats and refuge for fish and zooplankton, stabilise sediments and are involved in the nutrient cycling that improves the water transparency (Jeppesen *et al.*, 1998; Madsen *et al.*, 2001; Søndergaard *et al.*, 2003). Aquatic vegetation can inhibit the growth of microalgae by competition for nutrients and by allelopathic effects (Scheffer *et al.*, 1993; Nakai *et al.*, 1999). Thus, changes in macrophyte biomass may influence the aquatic ecosystem in many aspects.

Development of macrophytes is often analysed in the context of rising temperature during the growing season, which is often connected with the current climate change. The results are ambiguous and often related to the amplitude of water temperature (Barko *et al.*, 1982; Rooney and Kalff, 2000; Mckee *et al.*, 2002). Only very few studies have addressed the indirect effects of ice cover duration on the development of submerged vegetation (Hargeby *et al.*, 2004).

In the present study, we analysed the relationship between data on the ice break-up and biomass of submerged macrophytes in eutrophic lakes. We hypothesised that: i) the physicochemical parameters of water and phytoplankton abundance during the growing season are linked to the absence of ice or early ice-out on lakes; ii) macrophyte biomass during the summer season after mild winter is negatively affected by the high water turbidity induced by high phytoplankton abundance.

METHODS

The studies were conducted from 2010 to 2014 in four lakes, Czarne, Głębokie, Gumienek and Maśluchowskie located near the village of Uścimów in the Western Polesie region (mid-eastern Poland). With 67 lakes, Western Polesie is part of a large geographical region referred to as Polesie and divided between three countries: Poland, Ukraine and Belarus (Kondracki, 2002).

The studied lakes are small, shallow, eutrophic and situated in close proximity (Tab. 1). The lakes have similar susceptibility to changes in thermal conditions of water

Tab. 1. Morphometric characteristics of the studied lakes in the West Polesie region by Wilgat *et al.* (1991).

Lake	Coordinates	Area (ha)	Length (m)	Mean width (m)	Depth (m) max	Depth (m) mean	Volume (10^3 m³)	Mean slope inclination
Czarne	51° 29' 08" N 22° 56' 34" E	24.8	596	416	10.3	3.7	915	2° 20'
Głębokie	51° 28' 34" N 22° 55' 23" E	20.5	585	350	7.1	3.4	689	2° 10'
Gumienek	51° 30' 14" N 22° 56' 20" E	8.1	376	215	7.8	3.8	307	3° 50'
Maśluchowskie	51° 28' 03" N 22° 56' 43" E	26.7	861	310	9.4	4.6	1231	3° 00'

expressed by the lake area to lake volume ratio (Tab. 1), which ranged from 0.22 in Lake Maśluchowskie to 0.29 in Lake Głębokie. The water bodies are situated in the agricultural landscape. The catchment basins of the lakes Głębokie, Gumienek and Maśluchowskie consist of arable lands (20.5-73.5%), forests (0.57-23.9%) and meadows (4.67-7.57%). Lake Czarne has been surrounded by an earth dyke since the 1950s and has a largely limited area of the catchment basin (Ejankowski and Lenard, 2014).

Climatic data on air temperature and precipitation for a meteorological station in the town of Włodawa located in the Polesie region were taken from the online service (www.tutiempo.net). Mean air temperature for the periods of 14 days before sampling (T_{14}) and total precipitation of one hydrologic year before sampling, which strongly affects the water level of lakes in the Polesie region (Michalczyk *et al.*, 2010), were included in the analyses.

We assumed mid-March as an average time for winter ice cover breakup in Poland (Marszelewski and Skowron, 2006). The effects of the cold winter (CW) were studied in the years when the latest ice break-up date (L_{bd}) was observed later than mid-March, whereas the effects of the mild winter (MW) were studied when L_{bd} occurred before this period. Prior to calculations, ranks were assigned to average dates of ice-out in 2010-2014: 1=11-20 February; 2=1-10 March; 3=21-31 March; 4=1-10 April; 5=21-30 April. According to the differences between the two periods (CW and MW), the physicochemical parameters, the biomass of macrophytes and the amount of phytoplankton expressed by the concentration of chlorophyll-*a* were analysed.

Water sampling was conducted fortnightly, from May to the end of July (six samples per year in each lake, 120 samples in total). Mixed water samples were collected from depths of 0.5, 1.5 and 3 m from the sublittoral zone of the lakes with a Ruttner water sampler (2.0 L capacity). Then, they were analysed in a laboratory with the use of spectrophotometric methods to determine the concentration of chlorophyll-*a* (Nush, 1980), total phosphorus (TP), total nitrogen (TN), inorganic phosphorus (P-PO$_4$) and nitrogen (DIN=N-NO$_x$+N-NH$_4$) according to the procedures of Hermanowicz *et al.* (1999). The physicochemical parameters *i.e.*, electrolytic conductivity (EC), water reaction (pH) and transparency by Secchi disk visibility (SD) were measured *in situ*. Additionally, photosynthetic active radiation (PAR, I_z) was measured by a Li-Cor 192 SA underwater quantum flat meter. Then, the vertical light attenuation coefficient (K_d) between adjacent depth intervals (z and z+0.5 m) was calculated as:

$$K_d=(\ln(I_z) - \ln(I_{z+0.5m})) \ 0.5 \ m^{-1} \qquad \text{(eq. 1)}$$

where I_z is the PAR value of a depth z (Kirk, 1994).

The study of the submerged aquatic vegetation (SAV) in the lakes focused on changes in the biomass of macrophytes after the CW and the MW. The research was conducted at permanent study sites situated randomly in the phytolittoral zone of the lakes. The water depth of the macrophyte sampling depended on the extension of the vegetation in particular lakes. The study sites were marked in 2010 and located using a GPS receiver (Garmin 60Cx) in the consecutive years. Every year in August, 35-40 replicates were performed randomly in the phytolittoral of each lake with a rake sampler from 0.4 × 0.4 m quadrats. During 2010-2014, 765 samples of the SAV biomass were collected. Additionally, a water depth from the surface to the ground occupied by the sampled macrophytes was measured each time. Plants were cleaned, dried at a temperature of 105ºC to constant weight and weighed.

The data were log-transformed ($\log_{10}$ x+1) prior to analysis or non-parametric tests were used if data did not meet the assumptions of parametric tests. The normality of data was tested by the Lilleforst test and the homogeneity of variance was analysed by the Levene's test. Two qualitative categories - the CW and MW or rank system - L_{bd} were used depending on the type of statistical method. Fisher's test (F-test) in ANCOVA was employed to analysed the influence of factors: the type of winter (the CW and MW), the kind of lake and covariates: total precipitation of one hydrologic year and water depth of sampled macrophytes on the physicochemical and biological parameters. In the statistical models the total precipitation was insignificant and excluded from the following analyses. Thus, in the case of the physicochemical parameters and the concentration of chlorophyll-*a*, ANOVA was used to determine the effects of the CW and MW and kind of lake. Relationships between the parameters describing the water transparency (SD and K_d), phytoplankton (the concentration of chlorophyll-*a*) and nutrients (DIN, TN) were evaluated by non-parametric Spearman's correlation test, in which the rank system of L_{bd} was used . All calculations were performed according to Sokal and Rohlf (1995) using Statistica 10.

RESULTS

In the studied lakes in 2010-2014, the L_{bd} occurred in different periods of the year, and varied from the middle of February (winter period) to the end of April (spring period). After the CW, the L_{bd} was observed between 21 and 31 March (2012) or 1 and 10 and 21 and 30 April 2010 and 2013, respectively. After the MW in 2011 and 2014, early ice-out was observed due to relatively high mean air temperatures (www.tutiempo.net). The L_{bd} in 2011 occurred between 11 and 20 February and in 2014 between 1 and 10 March. During studies, total precipitation in one hydrologic year varied in a broad range, from 481.5 mm in 2013 to 717.6 in 2012. However, they were comparable in periods after the CW (636.2 mm) and the MW (629.1 mm).

During the course of the study, the concentration of total nitrogen (TN) and phosphorus (TP) changed simultaneously in all lakes. The alteration of both parameters corresponded with the extreme winters. The highest concentration and variation of TP values were measured in 2013 (the CW) and were very low in 2010-2012 and 2014. Only in a single case, Lake Głębokie, was the increase of TP concentration in 2013 less noticeable (Fig. 1a). On the other hand, the concentration of TN was the highest in 2011 (the MW) and much lower in the remaining years (Fig. 1b).

Other parameters differed considerably in particular lakes. Changes in the values of K_d in 2010-2014 presented a similar pattern as TN, with the maximum in 2011 and very high values in 2014, contrary to low K_d in 2010, 2012 and 2013 (Fig. 1d). The K_d values were negatively correlated with the SD visibility (Spearman's R=-0.84, P<0.001) and positively correlated with the concentration of chlorophyll-*a* in water (Spearman's R=0.88, P<0.001). The lowest K_d and concentration of chlorophyll-*a* and the highest SD values were recorded in Lake Czarne, whereas the highest K_d and chlorophyll-*a* and the lowest SD were observed in Lake Głębokie (Fig. 1 c,e).

The chlorophyll-*a* concentration increased with the mean air temperature ($T_{14\ days}$, Spearman's R=0.25, P<0.01) and slightly decreased with the ranged date of the latest ice break-up - L_{bd} (Fig. 2). The large dispersion of the chlorophyll-*a* in relation to L_{bd} in the scatter plot was caused by considerable differences between particular lakes (Fig. 2).

However, the mean values of chlorophyll-*a* were generally higher after the MW than the CW (Tab. 2).

In the studied lakes, many parameters corresponded to the type of winter. In spite of their high differences in particular lakes, expressed by standard deviations, the effects of CW and MW were revealed. In accordance with the concentration of chlorophyll-*a*, the K_d was higher and the SD was lower after the MW than after the CW (Tab. 2). The phytoplankton biomass was correlated with the elevated concentration of soluble (Spearman's R=0.21, p<0.05) and total nitrogen (Spearman's R=0.43, P<0.001). The water chemistry showed some differences between the two observed periods. After the MW, the values of TN, DIN and the ratio DIN/TN and TN/TP were higher, and the value of TP was lower than after the CW. Nonetheless, no differences in the electrolytic conductivity, P-PO$_4$ and pH were found between the compared periods (Tab. 2).

In the studied lakes, the SAV was composed mainly of three abundant species: *Ceratophyllum demersum* L., *Myriophyllum spicatum* L. and *Stratiotes aloides* L. (Fig. 3). The hornwort (*C. demersum*) was the most common macrophyte species in the lakes Głębokie, Czarne and Gumienek, whereas the water milfoil *M. spicatum* dominated over *C. demersum* in Lake Maśluchowskie. The water soldier (*S. aloides*) was abundant only in Lake Czarne (Fig. 3). Other species, such as *Potamogeton lucens* L., *P. acutifolius* Link, *P. natans* L., *Nuphar lutea* (L.) Sibth. & Sm. and *Elodea canadensis* Michx., were found only occasionally in the lakes.

Tab. 2. Mean values (±standard deviations) of submerged aquatic vegetation and particular macrophyte biomass, chlorophyll-*a* concentration (Chl-*a*) and physicochemical parameters in eutrophic lakes compared between the growing seasons after the cold and the mild winter in the best fitted models of ANCOVA or ANOVA. Selected effects related to the types of winter are presented below.

Parameter	CW	MW	df	F-test
Total SAV (g m^{-2})°	112.7 (±119.3)	77.9 (±100.1)	1	25.09***
Ceratophyllum demersum (g m^{-2})°	86.8 (±120.5)	70.4 (±98.9)	1	4.07*
Myriophyllum spicatum (g m^{-2})°	34 (±54.3)	11 (±16.4)	1	21.2***
Stratiotes aloides (g m^{-2})°	32.8 (±44.6)	15.6 (±28.4)	1	7.62**
Chl-a (μg L^{-1})#	18.9 (±14.6)	20 (±19.4)	1	5.62*
Kd (m^{-1})#	1.2 (±0.5)	1.5 (±0.7)	1	9.49**
SD (m)#	2.12 (±1.1)	1.98 (±1.1)	1	4.4*
Water temperature (°C)#	21.7 (±3.1)	21.1 (±2.7)	1	1.26
EC (μS cm^{-1})#	228 (±76.7)	232.7 (±83.5)	1	0.67
pH#	7.96 (±0.3)	7.97 (±0.3)	1	0.03
TN (mg L^{-1})#	1.9 (±0.8)	3.7 (±1.6)	1	78.5***
TP (mg L^{-1})#	0.18 (±0.2)	0.04 (±0.02)	1	14.53***
P-PO4 (mg L^{-1}) #	0.03 (±0.03)	0.01 (±0.05)	1	14.98***
DIN (mg L^{-1}) #	0.52 (±0.4)	2.08 (±1.2)	1	104.56***
DIN:TN#	0.3 (±0.3)	0.5 (±0.2)	1	26.61***
P-PO4:TP#	0.3 (±0.5)	0.3 (±2.3)	1	0.84
TN:TP#	31 (±24.7)	102 (±61.3)	1	75.01***

CW, cold winter; MW, mild winter; df, degree of freedom; SAV, submerged aquatic vegetation; Kd, attenuation coefficient; SD, Secchi disk visibility; EC, electrolytic conductivity; TN, total nitrogen; TP, total phosphorus; DIN, dissolved inorganic nitrogen. °ANCOVA; #ANOVA. *P<0.05; **P<0.01; ***P<0.001.

The average water depth of the macrophyte colonisation was 1.83 m in Lake Głębokie, 2.03 m in Lake Gumienek, 2.72 m in Lake Maśluchowskie and 3.04 m in Lake Czarne. In accordance with our assumptions, the biomass of macrophytes (SAV) decreased with water depth of sampling (ANCOVA, F=76.96, P<0.001) and increased with water transparency, SD (F=293.07, P<0.001). The negative effect of light limitation on the biomass macrophytes was noticeable in lakes Głębokie, Maśluchowskie and Gumienek. Only in Lake Czarne was
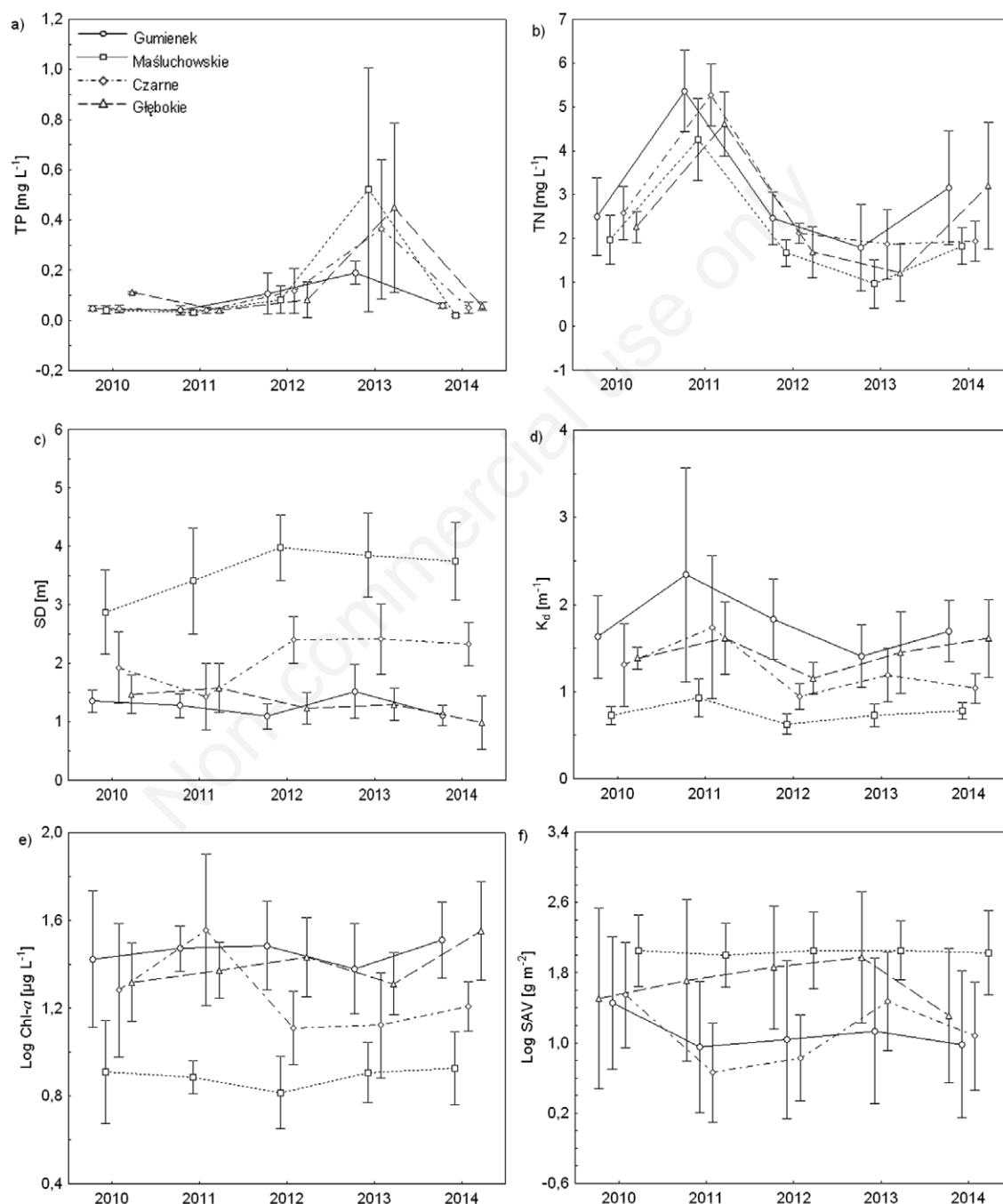

Fig. 1. Mean values (±standard deviations) of physicochemical and biological parameters of water in the studied lakes in 2010-2014. The concentration of chlorophyll-*a* (Chl-*a*) and the biomass of submerged aquatic vegetation (SAV) were log-transformed (log10 x+1). TP, total phosphorus; TN, total nitrogen; SD, Secchi disk visibility; K_d, attenuation coefficient.

the biomass of macrophytes constantly very high (Fig. 1f), in spite of considerable changes in the average seasonal (May-July) water transparency (SD) from 2.87 (2010) to 3.98 m (2012), the K_d from 0.69 (2012) to 0.95 (2011) and the concentration of chlorophyll-*a* from 5.95 (2012) to 8.37 µg L^{-1} (2014).

The abundance of the SAV in the periods following the CW and the MW corresponded with differences in the physicochemical and biological parameters. The total biomass of the SAV was much higher after the CW than after the MW (Tab. 2). This was reflected in the relatively high total biomass of the macrophytes in 2010 and 2013 (CW) and decreasing SAV in 2011 and 2014 (MW, Fig. 1f). The effect of winter (early or late ice-out) was important to all macrophyte species, but it was highly significant and much stronger in *Myriophyllum spicatum* and *Stratiotes aloides* than in *Ceratophyllum demersum* (Tab. 2, Fig. 3).

DISCUSSION

The projected climate warming will have a profound effect on the shortening of the duration and thickness of the ice cover (McCarthy *et al.*, 2001; Leppäranta, 2010; Livingstone *et al.*, 2010). The earlier ice-out on lakes determines changes in the physicochemical parameters, which are important to the abundant development of phytoplankton in spring (Weyhenmeyer *et al.*, 2008; Laugaste *et al.*, 2010; Nõges *et al.*, 2010). However, our results show that the effect of mild winters on lakes can also be observed in following growing season (Tab. 2).

In the studied lakes, the concentration of nutrients varied in the broad range and was determined by the winter periods. After the CW, a high concentration of total and soluble phosphorus in water was observed, whereas total and soluble nitrogen increased after the MW. Although the effects of CW and MW on nutrients were significant (Tab. 2), they were highly noticeable only after extreme warm (2011) and cold (2013) winters (Fig. 1 a,b). The values of TP and TN varied over time, whereas their changes among lakes were simultaneous (Fig. 1 a,b), which suggested the occurrence of a general external effect, most likely dependent on climatic conditions. Synchronous variations, however, in dissolved organic carbon and water colour affected by precipitation and data of ice-out were reported by Pace and Cole (2002). Nutrients concentration in water can also be influenced by precipitation, which could be a source of inorganic nitrogen from the atmosphere and enhanced surface runoff from the catchment basin, especially dominated by arable lands (Smal *et al.*, 2005; Hessen *et al.*, 2009). Our results showed that total precipitation linked with the CW and the MW was comparable and, in turn, should have a negligible effect on the highest or the lowest TP and TN concentrations. The alternative source of nitrogen in water could be the biological fixation of atmospheric N_2

by cyanobacteria (Howarth *et al.*, 1988; Cottingham *et al.*, 2015), however, these blue-green algae have never dominated in the studied lakes (Wojciechowska and Solis, 2009; unpublished data).

It seems that a stronger impact on low TP concentration could have short periods of ice cover, which affected the reduction of winter anoxia and the successive decrease of phosphate release from the sediments, as reported by other authors (Stefan and Fang, 1993; McCarthy *et al.,* 2001). In contrary, due to a long duration of ice cover, the increase of TP concentration in the studied lakes was recorded after the CW. On the other hand, based on the observations of Klimaszyk and Rzymski (2011), higher phosphorus concentration after the CW could be linked with increased surface runoff after snow and ice melting. Relatively high phosphorus concentration in the studied lakes after the CW could be associated with the agricultural land use in the catchment basin.
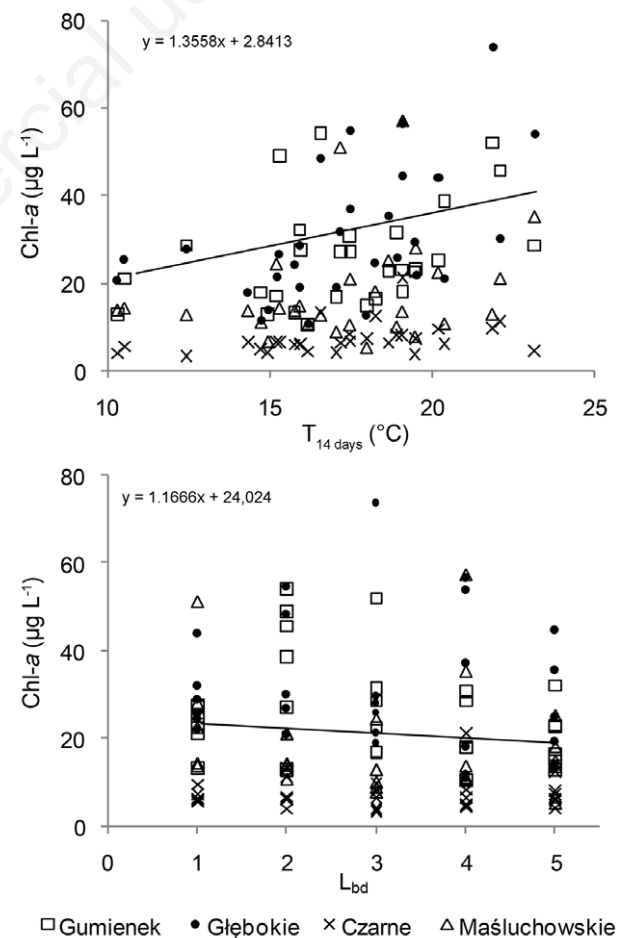

Fig. 2. Relationships between the concentration of chlorophyll-*a* (Chl-*a*) and the mean air temperature ($T_{14\ days}$), and ranges of the latest ice break-up date (L_{bd}) in the studied lakes.

We speculate that higher nitrogen concentration after the MW can be a result of a long period of wind-induced water mixing. The depth of effective water mixing in the lakes, calculated according to Patalas formula (1984) modified by Padisák and Reynolds (2003), varied from 2.7 m in Lake Gumienek to 4 m in Lake Maśluchowski and was often close to the mean water depths in lakes (Tab. 1). Intensified sediment resuspension accompanied by ice-free conditions in winter plays a major role as an internal supply of nitrogen in water, *e.g.*, $N-NH_4$, TN (Reddy *et al.*, 1996; Nõges *et al.*, 1998). Thus, in the studied lakes, the TN:TP ratio was considerably higher after the MW compared with the CW. This is consistent with other studies in shallow and deep lakes of Central and Northern Europe (Salmaso, 2002; Laugaste *et al.*, 2010) and inconsistent with the results from the different lakes of Western Europe, in which heavy winter rains tend to transport large portion of dissolved phosphorus into water (George *et al.*, 2004). Differences in other physicochemical parameters of water (EC, pH and temperature) were

statistically insignificant in growing seasons after the compared winter types (the CW and the MW).

The phytoplankton biomass is usually linked with increased nutrient concentration and temperature (Schindler *et al.*, 1990; Moss *et al.*, 2003). The thermal conditions influenced phytoplankton biomass in the studied lakes (Fig. 2); however, there was no difference in the mean water temperature after the CW and the MW (Tab. 2). According to our results, the more important factor determining high phytoplankton biomass, associated with ice cover duration on lakes, was the increased nutrient concentration. Consequently, light limitations induced by phytoplankton growth caused deterioration of submerged vegetation after mild winters. In contrast, high nutrient concentration and low phytoplankton biomass after mild winter was reported by Pełechata *et al.* (2015) in a small *Chara*-lake, in which the charophyte vegetation developed and strongly counteracted the excessive growth of phytoplankton. In the studied lakes in the Polesie region, which are phytoplankton- or macrophyte-dominated, non-
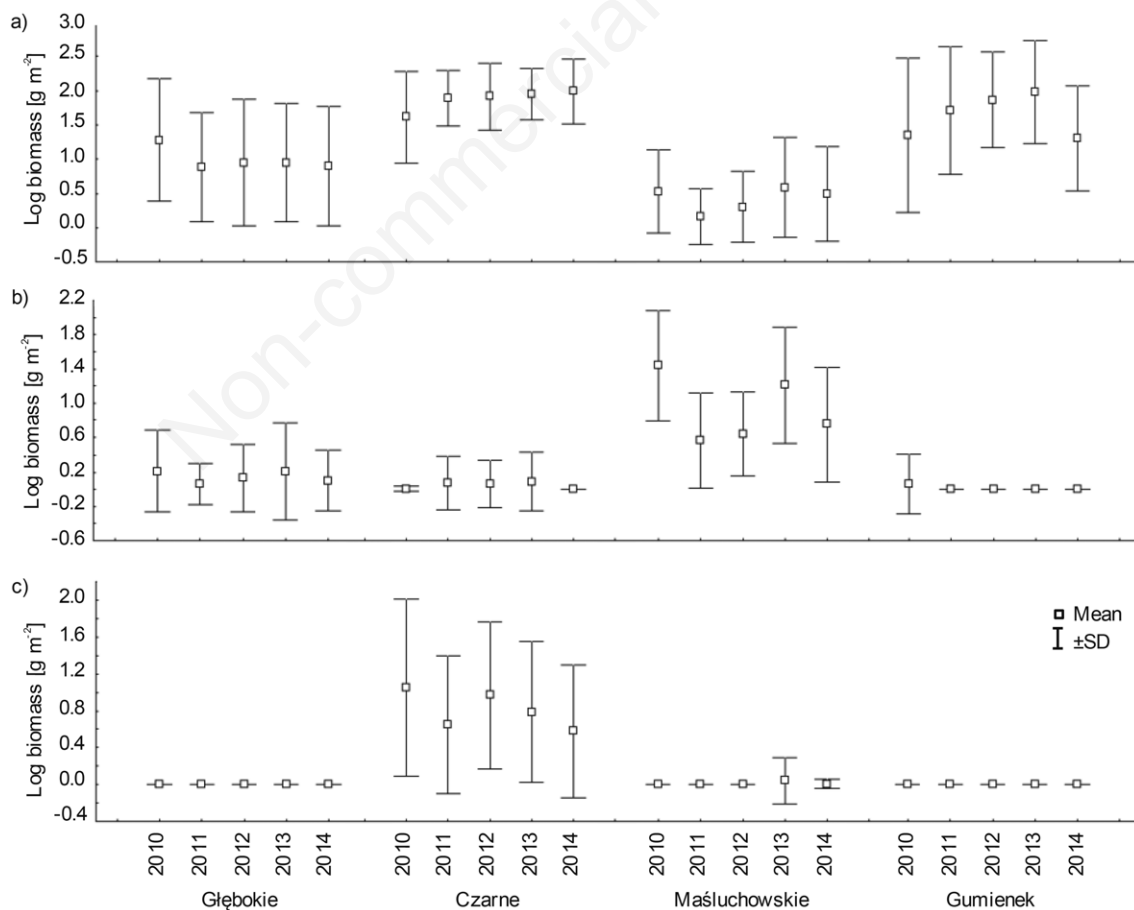

Fig. 3. Temporal variation in the log-transformed biomass ($\log_{10} x+1$) with standard deviations (±SD) of submerged macrophytes: a) *Ceratophyllum demersum*; b) *Myriophyllum spicatum*; and c) *Stratiotes aloides* in the studied lakes in 2010-2014.

overwintering species (*C. demersum*, *M. spicatum*) comprise benthic vegetation. Macrophytes such as milfoil and hornwort can influence the development of phytoplankton to a lesser extent than overwintering charophytes (van Donk and Van de Bund, 2002), which additionally reduce water turbidity (Casanova *et al.*, 2002).

Zooplankton grazing can reduce the abundance of phytoplankton in waters (Gyllström *et al.*, 2005; Jeppesen *et al.*, 2010). High water temperature in late spring has a strong impact on the emergence and development of zooplankton populations and can lead to an early clear water phase in lakes (Straile, 2000; Gerten and Adrian, 2000; Asaeda *et al.*, 2001). In the studied lakes, however, there were no differences in the mean water temperature between periods after the CW and the MW (Tab. 2), which suggests that the differences in zooplankton and phytoplankton development after both periods could be independent on thermal conditions. The temperature of water, however, affected the phytoplankton biomass during the growing season (Fig. 2). The grazing pressure on phytoplankton in shallow eutrophic waters, such as the studied lakes, is often negligible compared with deep mesotrophic ones (Jeppesen *et al.*, 1997). Moreover, the studied lakes are dominated by filamentous blue-green algae (Wojciechowska and Solis, 2009) that may affect the filtration capacity of zooplankton by interference and make them less edible (de Bernardi and Giussani, 1990). Thus, the variation in the concentration of chlorophyll-*a* between both winter periods was most likely independent on the grazing of zooplankton.

High concentrations of nutrients and chlorophyll-*a* in water resulted in changes in water transparency expressed by SD visibility and the values of K_d, which is consistent with the results of other studies (Tilzer *et al.*, 1995; Asaeda *et al.*, 2001). Poor underwater light climate in the studied lakes after the MW was stressful for the SAV, except for Lake Czarne, in which the biomass of SAV was continuously very high during the studies (Fig. 1f). In this lake, the highest values of water transparency and the lowest values of K_d were noted (Fig. 1 c,d). In Lake Czarne, a large part of the lake bottom (65%) is covered by macrophytes and submerged vegetation reached a depth (4.5 m) higher than the depth of effective water mixing (3.4 m). Additionally, the lake is surrounded by large belt of emerged vegetation that reduces wave action in the water body and indirectly limits sediment resuspension and improves water transparency. An inverse effect was found in other lakes, such as Głębokie, in which the maximum depth of macrophyte colonisation (2.5 m) was lower than the depth of effective water mixing (3.4 m). In this lake, a large part of the bottom (ca. 60%) was devoid of vegetation and exposed to turbulence (Ejankowski and Lenard, 2014). In Lake Czarne, macrophyte dominance could hamper the development of phytoplankton by different

mechanisms, *i.e.* competition on nutrients end allelopathic effects (Scheffer *et al.*, 1993; Nakai *et al.*, 1999; Pełechata *et al.*, 2015). According to other studies (Ali *et al.*, 1995, 2011; Ejankowski and Solis, 2015), we speculate that the light climate in this lake was still favourable for the SAV and much above the species tolerance level, independently on the type of winter.

Light conditions in lakes can be influenced by suspended particles and dissolved organic compounds, which affect water colour (Wetzel, 2001; Pace and Cole, 2002). Our findings are consisted with the observations of Blindow (1992) that the light climate for the development of SAV may be determined by water turbidity linked with particulate matter including phytoplankton. Interestingly, in the studied lakes, the effect of SD on the SAV was determined to be less important than K_d and the concentration of chlorophyll-*a*. This is because in highly eutrophic lakes with high water turbidity, SD values reflect the quality of the upper water layer only, whereas K_d and the concentration of chlorophyll-*a* were measured within the whole water column and reflected the light conditions from the water surface to the depth occupied by macrophytes. Considerable differences in the concentration of chlorophyll-*a* and the K_d through the water column were observed, in stratified lakes with a deep chlorophyll maximum (Micheletti *et al.*, 1998; Walsby *et al.*, 2001). Therefore, we suggest that K_d and the concentration of chlorophyll-*a* provide more precise data on the light climate for the SAV and more strictly results in the analysis of the relationships between light intensity and the development of macrophytes.

The conditions in the cold winter, in terms of a long period of ice cover combined with an increase in the ice thickness, are unfavourable to emergent aquatic macrophytes (Alahuhta *et al.*, 2011). On the contrary, submerged macrophytes were reported to be positively correlated with the duration of ice cover on a lake, as an effect of winter fish kill (Hargeby *et al.*, 2004). Long periods of ice cover may lead to winter fish kill that reduce predation pressure on zooplankton and consequently strengthen zooplankton grazing on phytoplankton (Gyllström *et al.*, 2005; Jeppesen *et al.*, 2010). Low phytoplankton biomass affects favourable light conditions in water and encourages the development of submerged macrophytes in a lake. During the five years of the study, the effect of anoxia under the ice cover has never been observed, which could be linked with a relatively high mean water depth (>3.4 m) in the lakes. Therefore, the impact of winter fish kill can be omitted in the studied lakes.

Changes in the environmental conditions in lakes, such as the concentration of nutrients, the light climate and the water level, can result in the abundance and composition of SAV (Wallsten and Forsgren, 1989; Blindow, 1992; Ejankowski and Solis, 2015). Responses to light

conditions of SAV may vary in particular macrophyte species (Nurminen, 2003). In the studied lakes, the light deficiency related to an increase in water turbidity after the MW had a strong negative effect on the macrophytes, which are moderately light-demanding species (Zarzycki *et al.*, 2002). The stronger effect on *Myriophyllum spicatum* L. and *Stratiotes aloides* L. than on *Ceratophyllum demersum* L. can be explained by their lower tolerance to water turbidity (Haslam, 1997; Szoszkiewicz *et al.*, 2010). The shade tolerance of *C. demersum* seems to be the main factor responsible for the relatively high abundance and common occurrence of this species in many turbid water bodies (Ali *et al.*, 1995, 2011). Deteriorated water quality had a relatively small effect on the abundance of the hornwort that can potentially determine its strong competition ability in the lake ecosystems.

CONCLUSIONS

Our findings show that the term of ice cover melting, acting through the concentration of nutrients, the phytoplankton biomass and water turbidity, affects the biomass of the SAV in the lakes. Thus, cold and mild winters can change the balance between the phytoplankton and benthic vegetation in shallow eutrophic lakes, as a shift between the clear and turbid water states in terms of the alternative state theory proposed by Scheffer *et al.* (1993). We speculate that various responses of particular macrophytes to changes in the water quality after the cold or mild winters could be a cause of the alterations in the vegetation structure, particularly, the expansion of shade-tolerant species instead of light-demanding ones after a series of mild winters.

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