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## EFFECT OF LIGHT COMPETITION WITH FILAMENTOUS ALGAE ON THE POPULATION DYNAMICS AND DEVELOPMENT OF THE MOSS SPECIES *WARNSTORFIA EXANNULATA* IN A SOFTWATER LAKE

**ABSTRACT:** The effect of a massive bloom of filamentous algae on the long-term abundance dynamics of the moss *Warnstorfia exannulata* (B., S. & G.) Loeske was studied in an acidic low-productivity lake in NW Poland. Individuals were counted on 4 experimental plots, 1 × 1 m each, at a depth of 2.5 m. The studies were conducted for 36 months, every 30 days, by SCUBA diving. Over the three years the seasonal changes in water pH, conductivity, HCO<sub>3</sub><sup>-</sup> concentration, sediment hydration and pH were not statistically significant ( $P > 0.05$ ), and light intensity was higher in winter than in summer.

Over the three years 4 consecutive stages of population development were observed: regeneration, stabilisation of abundance (fluctuations), regression and repeated regeneration. These stages appeared and lasted at different temperatures and light intensity. The greatest monthly increase in abundance took place in summer and lasted until the beginning of autumn under conditions of high temperature and relatively low light intensity. Long-term abundance variations were strongly correlated with the appearance of filamentous algae, less strongly with the dynamics of the dominant species (*Sphagnum denticulatum*), and the least with water temperature, light intensity, water and sediment pH, conductivity and HCO<sub>3</sub><sup>-</sup> concentration. As a result of a massive bloom of these algae, light intensity decreased in the water, *Warnstorfia* shed its leaves, and then the entire population disappeared. In winter that year it began to regenerate

from vegetative propagules (leafless shoots), which were the remains of individuals growing before the filamentous algae appeared. In softwater lakes such massive algal blooms are a common phenomenon which limits light transmission to the substrate and as a result leads to changes in the submerged vegetation structure, especially that of bryophytes.

**KEY WORDS:** aquatic moss population, *Warnstorfia exannulata*, population dynamics, filamentous algae, softwater lake

### 1. INTRODUCTION

Submerged mosses are a frequent component of plant communities in the softwater lakes (<3.0 mg Ca L<sup>-1</sup>, pH <6.0) of northern Europe (Murphy 2002). They occur alone, with higher plants or charophytes and mainly form thick carpets (Srivastava *et al.* 1995, Toivonen and Huttunen 1995, Bociąg 2003, Szmeja 2009), which are important regulators of the exchange and cycling of nutrients (Jaynes and Carpenter 1986, Roelofs 1983, Catling *et al.* 1986). Aquatic mosses also perform a crucial function of sediment formation, due to which they are studied not only by botanists, ecologists or limnologists, but also paleobotanists, paleolimnologists and sedimentologists.

The carpets in acidic and softwater lakes are made up of perennial and evergreen mosses, whose structure and population dynamics, with just a few exceptions, have not been analysed. *Warnstorfia exannulata* (Schimp. in B.S.G.) Loeske (syn.: *Drepanocladus exannulatus* (Br. Eur.) Warnst., *Hypnum exannulatum* Br. Eur., *Amblystegium exannulatum* DNot., *Hypnum fluitans* ssp. *exannulatum* Dix.) is one of such aquatic mosses. It occurs in Europe, North, West and Central Asia, North America, Greenland, Falkland Islands and New Zealand (Nyholm 1965), so the geographical range of this species is very wide. In northern Poland (Pomerania) it grows in low-productive lakes, in communities with *Sphagnum cuspidatum* Ehrh. ex Hoffm. and *S. fallax* (Klinggr.) Klinggr. (Gos *et al.* 2007), as well as *Juncus bulbosus* L., *Lobelia dortmanna* L., *Isoetes lacustris* L. and others. A usually massive bloom of filamentous algae, which may considerably affect the population dynamics of submerged macrophytes, especially mosses, is a frequent phenomenon in summer in such lakes.

The Bory Tucholskie National Park (Pomerania region, NW Poland) is one of the areas where *W. exannulata* is a common species. The park encompassing 4613 ha was established in 1996 to protect pine forests (79% of the park's area), lakes and peatlands (11%). It is situated on a vast outwash plain formed during the last glaciation. The mean annual air temperature in this area is +7.1°C, with July being the warmest month (+16.7°C) and January the coldest (-2.6°C). The annual precipitation total is 577 mm. The lowest precipitation is recorded in winter (February) and the heaviest in high summer (July). The sandy, very acidic soils dominant in the catchment are poor in nitrogen and phosphorus and have low buffer and sorptive properties (Szmeja 2009).

We have formulated the following study hypothesis: environmental conditions (temperature, light intensity, water and sediment) affect the seasonal variation in population abundance to a lesser extent than the competition on light with *Sphagnum denticulatum* Brid. and filamentous algae. To test this the long-term observations of *Warnstorfia exannulata*, *Sphagnum denticulatum* and filamen-

tous algae populations were made in a small natural softwater lake with clear and acidic water located in a well-preserved pine-forest catchment.

## 2. METHODS

The *Warnstorfia* population was examined in Lake Gacno Wielkie (NW Poland, 120 km to the SW of the Gulf of Gdańsk) every month from August 2004 to July 2007 on 4 permanent plots, 1 × 1 m each, divided into 0.2 × 0.2 m quadrats at a depth of 2.5 m. For 36 months, *Warnstorfia* individuals were counted by a diver, and water temperature (°C), pH, conductivity (µS cm<sup>-1</sup>), colour (mg Pt L<sup>-1</sup>), PAR intensity (% of light reaching the population) and HCO<sub>3</sub><sup>-</sup> concentration (mg L<sup>-1</sup>) were measured on the 4 plots. In spring, summer, autumn and winter (once every season), sediment samples were collected to plastic containers with a volume of 250 cm<sup>3</sup> (144 samples in total) near the plots. In the sediment samples, pH, conductivity (µS cm<sup>-1</sup>) and redox potential (mV) were determined. The analyses were performed using the methods recommended by Hermanowicz *et al.* (1999), Wetzel and Likens (1991) and Eaton *et al.* (2005). The significance of differences between the samples was tested by ANOVA (Kruskal-Wallis test) (Łomnicki 1999) for *P* < 0.05. The population growth rate (PGR; individuals m<sup>-2</sup> month<sup>-1</sup>) was calculated from the difference in the number of individuals on the 4 plots (4 m<sup>2</sup>) between the successive months.

Some published data on the population abundance of *Sphagnum denticulatum* were used in this work. They come from the same experimental plots and time periods as those on *Warnstorfia* (Szmeja 2009).

## 3. RESULTS

Lake Gacno is small (13.5 ha), shallow (5.5 m), oligotrophic, acidic, softwater and free from considerable human pressure. The experimental plots were situated at a depth of 2.5 m (Table 1) on an acidic (pH 4.3–5.7), mineral (3.4 ± 2.6% of organic matter) and poorly hydrated (33.8 ± 9.8%) substrate with a low, but very variable redox potential (between -228 and +396).

Table 1. Water properties of Lake Gacno on study plots (arithmetic means with standard deviation, 3 measurements of each property for each month, in 2004 – 2007).

Month	Temperature [°C]	PAR [%]	pH	Conduct. [ $\mu\text{S cm}^{-1}$ ]	Colour [mg Pt L <sup>-1</sup> ]	HCO <sub>3</sub> <sup>-</sup> (mg L <sup>-1</sup> )
April	10.0 ± 3.0	26.7 ± 7.1	4.8 ± 0.1	31.2 ± 0.7	6 ± 1	41.2 ± 6.7
May	16.3 ± 0.6	21.3 ± 6.8	5.1 ± 0.2	22.6 ± 0.7	5 ± 0	32.3 ± 3.3
June	21.7 ± 2.5	17.0 ± 3.6	5.6 ± 0.5	29.5 ± 3.7	9 ± 1	33.7 ± 15.3
July	23.3 ± 2.1	16.0 ± 6.1	6.1 ± 0.2	27.6 ± 0.8	12 ± 2	16.9 ± 1.3
August	20.3 ± 1.1	11.0 ± 7.8	6.0 ± 0.2	23.2 ± 0.5	11 ± 1	23.0 ± 3.4
September	17.0 ± 0.1	11.0 ± 5.3	6.0 ± 0.1	32.0 ± 2.1	10 ± 2	28.2 ± 4.4
October	11.7 ± 2.1	17.7 ± 5.0	4.8 ± 0.5	25.2 ± 1.7	8 ± 1	15.9 ± 1.2
November	5.3 ± 1.5	20.3 ± 7.0	5.7 ± 0.3	30.5 ± 12.5	6 ± 2	28.2 ± 4.2
December	3.0 ± 1.7	25.3 ± 5.7	6.3 ± 0.6	40.9 ± 13.7	8 ± 1	70.2 ± 24.0
January	3.7 ± 1.1	24.0 ± 6.9	5.6 ± 0.2	37.9 ± 21.8	8 ± 1	44.1 ± 10.7
February	3.7 ± 1.5	24.0 ± 5.0	5.4 ± 0.1	21.6 ± 1.9	7 ± 1	38.4 ± 3.9
March	5.7 ± 2.1	25.7 ± 6.5	5.0 ± 0.1	23.8 ± 1.0	7 ± 1	46.5 ± 6.1

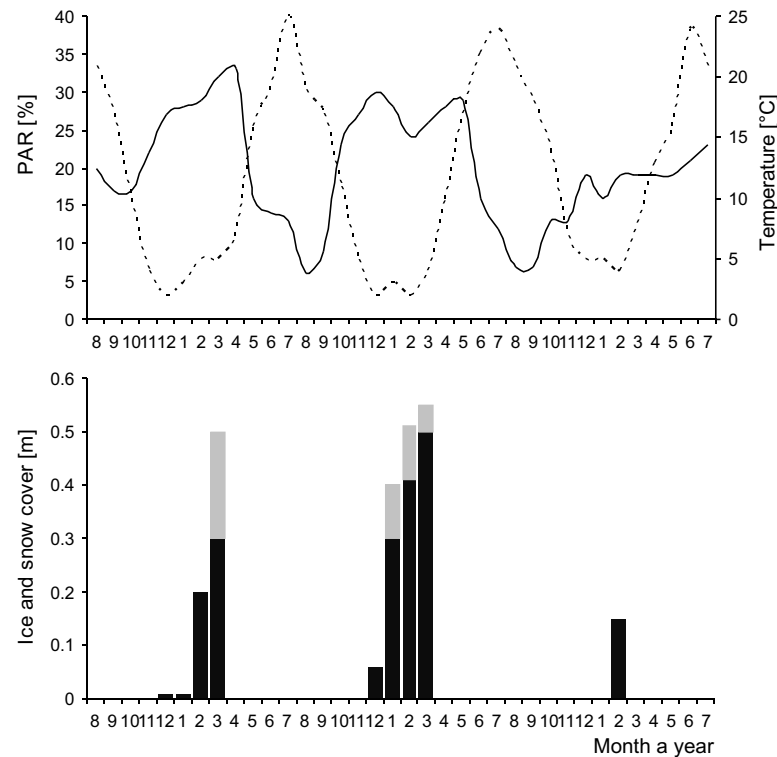


Fig. 1. PAR intensity (continuous line), water temperature at depth 2.5 m (dotted line), ice cover (black bar) and snow cover (grey bar) thickness in consecutive months from August 2004 to July 2007.

Based on water temperature measurements, the following time periods were established for the seasons in Lake Gacno: spring (April, May;  $13.2 \pm 4.0^\circ\text{C}$ ), summer (June–August;  $21.8 \pm 2.2^\circ\text{C}$ ), autumn (September, October;  $14.3 \pm 3.2^\circ\text{C}$ ) and winter (November–March;  $4.3 \pm 1.7^\circ\text{C}$ ). Water temperatures in spring (April  $10.0 \pm 3.0^\circ\text{C}$ , May  $16.3 \pm 0.6^\circ\text{C}$ )

and autumn (October  $11.7 \pm 2.1^\circ\text{C}$ , November  $5.3 \pm 1.5^\circ\text{C}$ ) were fairly varied, whereas in summer and winter much more stable. The first (2004/2005) and second (2005/2006) winters were quite frosty, while the third one (2006/2007) was mild.

Light intensity in water was seasonally variable: in winter higher than in summer

(Fig. 1). The numerical values of water colour were higher in summer than in the other seasons. Both these water properties indicate that in summer less light reached the population than in the remaining time periods, which was mainly due to the presence of plankton and epiphytic algae. A massive bloom of these algae took place in summer 2006. Over the three years the seasonal variations in water pH, conductivity, and  $\text{HCO}_3^-$  concentration were not statistically significant ( $P > 0.05$ ).

The variability of sediment properties (hydration, pH, conductivity and redox) was also statistically insignificant. It should be noted that  $\text{HCO}_3^-$  concentration was higher in winter ( $43.2 \pm 16.0 \text{ mg L}^{-1}$ ) than in summer ( $20.3 \pm 13.6 \text{ mg L}^{-1}$ );  $P < 0.05$ .

For the three consecutive years *Warnstorfia* occurred in small numbers on the experimental plots. *Sphagnum denticulatum*, accompanied by *Isoetes lacustris* L., *Lobelia dortmanna* L., *Juncus bulbosus* L. and *Spar-*

Table 2. Number of *Warnstorfia exannulata* individuals per 1 m<sup>2</sup> on I-IV plots in the study years and average population growth rate (PGR; individuals m<sup>-2</sup> month<sup>-1</sup>).

Year	Month/plot	I	II	III	IV	PGR
2004	August	0	0	0	0	0
	September	0	0	0	0	0
	October	0	0	0	0	0
	November	0	0	0	0	0
	December	0	0	0	0	0
	January	0	0	0	0	0
2005	February	2	0	0	0	0.5
	March	0	0	0	0	0
	April	1	0	0	7	2.0
	May	9	10	0	19	7.5
	June	16	13	17	64	18.0
	July	57	34	17	62	15.0
	August	46	29	16	60	-4.7
	September	67	30	21	72	9.7
	October	81	48	17	79	8.7
	November	45	39	19	71	-12.2
	December	49	42	13	74	1.0
	2006	January	41	38	18	63
February		43	37	18	53	-2.2
March		72	43	14	61	9.7
April		66	29	16	60	-4.7
May		57	26	13	45	-7.5
June		50	18	3	43	-6.7
July		3	0	1	1	-27.2
August		1	0	0	2	-0.5
September		0	0	0	0	-0.7
October		0	0	0	0	0
November		0	0	0	0	0
December		0	0	0	0	0
2007	January	0	0	0	0	0
	February	5	1	2	24	8.0
	March	0	1	0	28	-0.7
	April	16	4	0	37	7.0
	May	8	2	8	17	-5.5
	June	9	5	6	11	-1.0
	July	7	4	6	8	-1.5

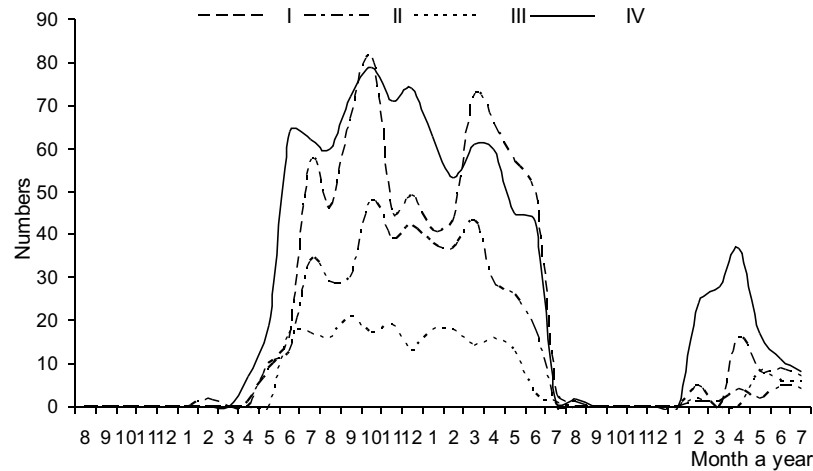


Fig. 2. The number of individuals of *Warnstorfia exannulata* per  $m^2$  on I – IV plots in consecutive months (from August 2004 to July 2007).

*ganium angustifolium* Michx., was the dominant species.

From mid-August 2004 to mid-May 2005, that is for 10 months from the beginning of the observations, 2–45 *Warnstorfia* individuals grew on the plots (Fig. 2). Winter 2004/2005 was frosty (Fig. 1) and consequently water was cold in April (7°C). A lot of light reached the plots (33% PAR). In May water temperature was much higher (16°C), but light intensity fell (17% PAR). In summer (June, July), a strong upward trend in the population abundance, which continued until the end of spring 2006, was observed. During frosty and snowy winter 2005/2006, which lasted in the lake from November to mid-March, the population abundance fluctuated and remained at a similar level to the one from the previous autumn. In the middle of the warm summer (water temperature in July 24°C, 12% PAR), owing to the massive bloom of filamentous algae, the abundance of *Warnstorfia* decreased from 114 in June to zero individuals in September. From July 2006 to January 2007 photosynthesising individuals were not present on the plots. They reappeared in February, and until July (the end of the observations) their abundance remained at a similar level.

Four development stages were distinguished in the *Warnstorfia* population: (1) regeneration (August 2004–May 2005); (2) stabilisation of abundance (June 2005–June 2006); growth (June–October 2005), slight

fluctuations (November 2005–February 2006), repeated growth (March 2006) and abundance decrease (April–June 2006); (3) regression (July 2006–January 2007); and (4) regeneration: from February to the end of the observations in July 2007 (Table 2, Fig. 2). These stages occurred and lasted at different temperatures and light intensity.

The population abundance fluctuated during the stabilisation stage. The dynamics of these changes were small for a perennial plant that reproduces vegetatively like the studied one. The upward trend continued for a maximum of 4 months (April–July 2005). The highest monthly growth rates of individuals (PGR) occurred from summer to the beginning of autumn, that is from June to October 2005 (Fig. 3), under conditions of high temperature and relatively low light intensity (Table 1).

*Warnstorfia* formed a small fraction on the experimental plots, where *Sphagnum denticulatum* was the dominant species (Fig. 4). From June 2005 to March 2006 both the populations were in the stage of abundance stabilisation, which makes the comparison of their development patterns possible. Both the increase (+PGR) and decrease (–PGR) in *Warnstorfia* population abundance occurred at various water temperatures, light intensity, water and sediment pH, conductivity and  $HCO_3^-$  concentration (Table 1). It seems that the abundance dynamics of *Warnstorfia* was not dependent on physical or chemical water

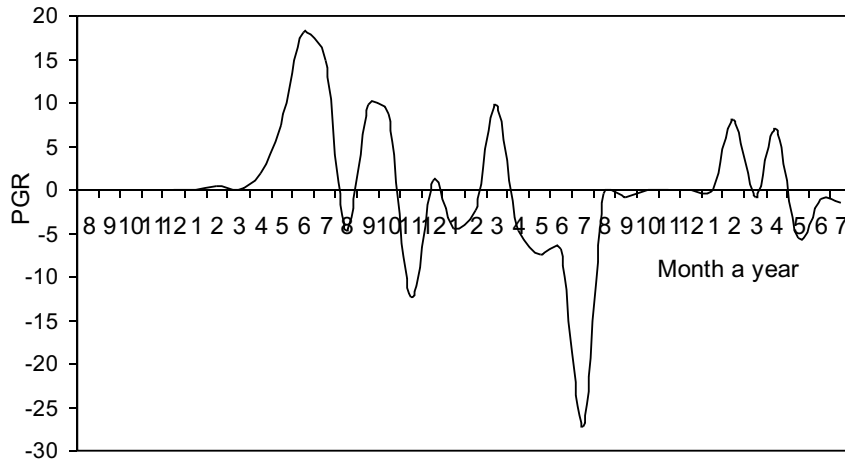


Fig. 3. Variability of the population growth rate (PGR; indiv. m<sup>-2</sup> month<sup>-1</sup>) of *Warnstorfia exannulata* over time, from August 2004 to July 2007.

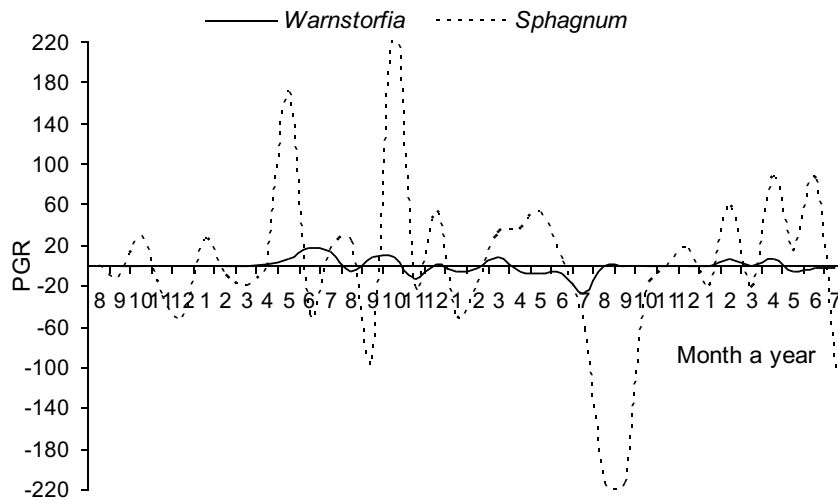


Fig. 4. Variability of the population growth rate (PGR; indiv. m<sup>-2</sup> month<sup>-1</sup>) *Warnstorfia exannulata* and *Sphagnum denticulatum* over time, from August 2004 to July 2007.

or sediment properties. However, it was synchronised, albeit not precisely, with analogous changes in the dominant species in the moss carpet (*Sphagnum*). In summer 2005 (June-September), the increase and decrease in both the populations, determined month by month, took place independently: one population increased and the other decreased in size. On the other hand, in autumn, winter and spring (October 2005-March 2006), the growth and reduction of both these populations were synchronised, that is both grew

and were reduced in size at the same time. The highest monthly population growth rate of *Sphagnum* was recorded at a fairly low temperature and good lighting (in May and October), while that of *Warnstorfia* at a relatively higher temperature and worse lighting (in May and October).

Winter 2005/2006 was long and frosty (4–5°C – water temperature from November to March), whereas spring very warm (10°C in April, 17°C in May). From mid-March to mid-May, that is over 60 days, water tem-

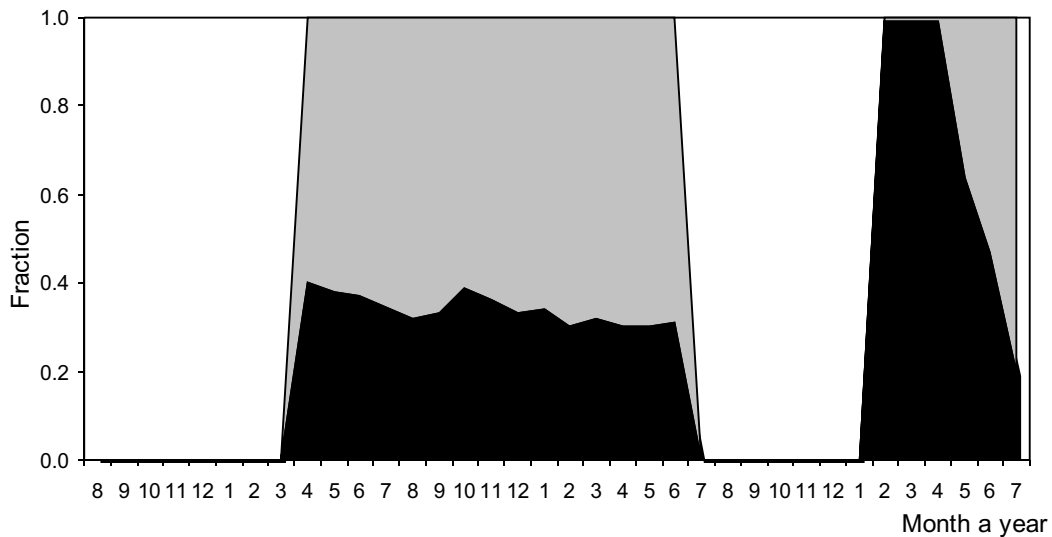


Fig. 5. Fraction of juvenile (black) and mature (grey) individuals in consecutive months from August 2004 to July 2007.

perature increased by 13°C (0.2°C/day). The beginning of summer was also warm (22°C in June, 24°C in July). Such conditions facilitated a massive bloom of filamentous algae, whose dense mats eliminated all *Warnstorfia* individuals from the plots within a short time.

The process of population vanishing (regression) lasted from July 2006 to January 2007, that is half a year. On the plots, 200 *Warnstorfia* individuals grew in March 2006, 151- in May, and only 5- in July (Table 2). From mid-June to mid-July 2006, that is over 30 days, under conditions of high water temperature, low light intensity (14–16% PAR) and proliferation of filamentous algae, the number of *Warnstorfia* individuals rapidly decreased (PGR:  $-27.7$  indiv.  $m^{-2}$  month $^{-1}$ ), their communities thinned and then a complete disintegration of the population took place. All the shoots shed their leaves during this process. At the same time, most *Sphagnum* individuals also perished on the plots. Over the next few months the leafless shoots of both these mosses lay on the sediment surface. It is worth mentioning that the filamentous algae were present in the summer of each year, but were less numerous and led to less severe consequences in both the populations.

The regeneration of *Warnstorfia* population began in February 2007 (Table 2) at a water temperature of 3.0°C and light intensity PAR of 19%. By April the population abun-

dance successively increased, whereas from the warming period in spring to the end of the study in July it fluctuated. In June and July the population was reduced in size (Fig. 3, 4), as the filamentous algae reappeared in the lake, albeit with less intensity than in the summer of the previous year.

The fraction of juveniles in the population, presented on a scale of 0 to 1.0 (Fig. 5), was varied. In the stabilisation stage of the population size (May 2005–June 2006) the juvenile fraction oscillated around 0.25, it was absent during regression (July 2006–January 2007), and it grew in the regeneration stage (February–July 2007). The population regenerated from the leafless shoots that had grown on the plots before the regression stage and performed the function of vegetative diaspores. The process of regeneration began in winter (February, PGR +8.0) and progressed slowly (Table 2).

#### 4. DISCUSSION

In softwater lakes *Warnstorfia exannulata* is a component of a submerged moss carpet and it occurs with other bryophytes with which it competes for light, nutrients and available space. The analysis of long-term changes in the population abundance of this plant may result in the explanation of the moss carpet dynamics.

In north-west Poland moss carpets are found in small softwater lakes with isoetids, such as *Lobelia dortmanna*, *Isoetes lacustris* and *Luronium natans* (L.). The studied lake (Lake Gacno Wielkie) is situated on a vast outwash plain from the time of the last glaciation covered with acidic soils (Chmara 2008), which make it acidic as well. There is no sufficient reason to associate the occurrence of the moss carpet in Lake Gacno with anthropogenic acidification, as it was the case in the lakes described by Grahn *et al.* (1974), Grahn (1977), Roelofs (1983) or Raven (1988) for example.

In Lake Gacno the experimental plots lay within the moss carpet at a depth of 2.5 m, were well-lit (11.0–26.7% PAR), occupied an acidic (pH 4.3–5.7), mineral ( $3.4 \pm 2.6\%$  of organic matter) and poorly hydrated ( $33.8 \pm 9.8\%$ ; Table 1) substrate. The structure of submerged vegetation was similar to the one in Danish Lake Grane Langsø (Riis and Sand-Jensen 1997) and some Karelian lakes (Ilyashuk 2002). It is possible that in each of these lakes the variation mechanism of *Warnstorfia* abundance is similar.

Long-term abundance changes depend on the development pattern of the moss carpet to a greater extent than on the seasonal variations of physical and chemical water and sediment properties (Table 1, 2, Fig. 2, 3, 4). In Lake Gacno the moss mat was seasonally disturbed. For instance, after a drop of water level in the lake the shallow zone of the mat was destroyed by waves, whereas after a rise in water level the zone close to the bottom (deep) limit was cut off. A similar phenomenon was observed near the shallow and deep limits of *Isoetes lacustris* and *Lobelia dortmanna* population ranges (Szymeja 1994). From time to time the moss carpet vanishes completely, due to the massive bloom of filamentous algae in Lake Gacno for example. This was the case during scorching summers after warm springs. Ellis-Evans and Walton's (1990) studies indicate that some filamentous algae do not tolerate low temperatures. Nevertheless, some of them survived the winter in Lake Gacno. A similar phenomenon was observed by Hawes (1989, 1990). Another cause of seasonal regression of *Warnstorfia* populations is rapid sediment resuspension after a considerable drop of water level, as

was the case in Lake Krasne situated a few dozen kilometres from Lake Gacno. In both these lakes the moss mat regenerated: in Lake Krasne the process took place over a period of less than 2 years, while in Lake Gacno 30% of the biomass was reconstructed as soon as after 5 months (Szymeja 2009).

*Warnstorfia* does not produce spores and consequently the recruitment of young individuals to the population is only vegetative. Juveniles appear all year long, irrespective of temperature or light intensity, and represent 20–25% of the fraction (Fig. 5). It is worth mentioning that the young individuals of the dominant species in the moss carpet (*Sphagnum denticulatum*) appear only once a year in spring (6.0–16.0 °C, 19.6–30.0% PAR) and make up 30–40% of the fraction, but their abundance is several times greater than that of *Warnstorfia*. From August 2004 to April 2005, 305–623 *Sphagnum* individuals (Szymeja 2009) and only 2–17 *Warnstorfia* individuals grew on the plots (Fig. 2). One of the significant causes of the domination of *Sphagnum* is its constantly abundant juvenile fraction.

Submerged mosses grow fast, in summer much faster than in winter, but live short: from 0.7 to 2.9 years (Riis and Sand-Jensen 1997). The annual growth rate of *Sphagnum* is  $45.3 \pm 5.9$  mg air-dry weight shoot<sup>-1</sup> year<sup>-1</sup> at a depth of 6.0 m in some softwater lakes of Karelia (Ilyashuk 2002), whereas in Danish Lake Grane Langsø  $17.9 \pm 2.2$  mg air-dry weight shoot<sup>-1</sup> year<sup>-1</sup> (Riis and Sand-Jensen 1997). High values of the elongation rate of this plant in Lake Grane Langsø ( $251 \pm 7$  mm shoot<sup>-1</sup> year<sup>-1</sup>) and in the Karelian lakes ( $189 \pm 7$  mm shoot<sup>-1</sup> year<sup>-1</sup>) confirm the fact that it grows fast. *Warnstorfia* grows just as fast:  $248 \pm 59$  mm shoot<sup>-1</sup> year<sup>-1</sup> and  $14.2 \pm 3.7$  mg air-dry weight shoot<sup>-1</sup> year<sup>-1</sup> (*op. cit.*).

The values of the population growth rate of *Warnstorfia* (Table 2) are lower than those of *Sphagnum* (Szymeja 2009). In Lake Gacno the growth of *Warnstorfia* depends on reproductivity and mortality of the population as well as competition, especially from the filamentous algae and to a lesser extent from *Sphagnum*. The population dynamics of *Warnstorfia* may also depend on carbon and oxygen cycling (Welch and Kalff 1974, Bates 1992, Srivastava *et al.* 1995) and

nutrient enrichment in the hypolimnion during summer stratification (Riis and Sand-Jensen 1997).

Juveniles appear all year round (Fig. 5). A certain fraction develops from fragments of leafless shoots lying on the sediment or under a thin sediment layer. Temperature rise and high light intensity in spring stimulate their growth. Leafless shoots are viable and able to regenerate, which is an adaptation to seasonally low light intensity and long-term low temperatures. In Lake Gacno, the arithmetic mean of water temperature is  $4.3 \pm 1.7^\circ\text{C}$  from November to March, that is for 5 consecutive months. The elongation of shoots of aquatic mosses also takes place in winter (Riis and Sand-Jensen 1997, Ilyashuk 2002), which means that low temperatures do not induce their diapause (Priddle 1980). The filamentous algae, which overshadow the mosses beneath them and are a light filter, may be the triggering factor of this phenomenon resulting in leaf-shedding. The algae also compete for nutrients and available space (Ozimek *et al.* 1991, Szmeja 1994, 2006). The all-year-round viability of the vegetative diaspore bank (leafless shoots) and the seasonal modification of light intensity by the filamentous algae are significant regulators of *Warnstorfia* abundance in Lake Gacno. The filamentous algae twine round *Warnstorfia* shoots and in this way reduce the light energy that reaches the moss. This indicates one-sided competition for light without signs of contending for space.

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