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THE INFLUENCE OF CO-OCCURRING VEGETATION AND HABITAT VARIABLES ON DISTRIBUTION OF RARE CHAROPHYTE SPECIES *LYCHNOTHAMNUS BARBATUS* (MEYEN) IN LAKES OF WESTERN POLAND

ABSTRACT: At present *Lychnothamnus barbatus* (Meyen) Leonhardi belongs to the rarest species of charophytes in the world. In Europe it is classified as threatened with extinction. The problem of extinction of this species is intriguing, in particular in the context of its widespread occurrence in Europe and Asia till the last decade of the 20th century.

Records of *L. barbatus* from Wielkopolska region (Western Poland) are know from 15 lakes. The most of them was stated in 19th and on beginning of 20th centuries. Now, this species is growing in 6 lakes, from among 2 sites are new.

This study was undertaken to a) determine the abundance of *L. barbatus* and the co-occurring plant species at different sites in lakes, b) determine the most important ecological parameters controlling the structure communities with *L. barbatus* co-occurring and quantitative responses of this species.

In 7 lakes (area 5.5-197 ha, depth max. 7.8–38 m, trophic state: meso-eutrophic) in western Poland the species composition and coverage of vegetation were studied at the 23 plots with *L. barbatus* occurrence in relation to the measured variables. Seventeen environmental parameters were measured including: depth of water, pH, conductivity, SO_4^{2-}, NH_4^+, NO^{3-}, PO_4^{3-}, Na^+, K^+, Ca^{2+}, Mg^{2+}, chlorophyll *a*, Secchi disc visibility, colour, O_2 dissolved, saturation, total Fe during the period July–September. The DCA and CCA analyses were used to assess the relation between vegetation parameters and environmental variables. *L. barbatus* preferred the water rich in Ca^+, Mg^{2+} and SO_4^{2-} and with high concentrations of nutrients, especially NH_4^+ and PO_4^{3-}, and moderate values of electrolytic conductivity. In the studied lakes, *L. barbatus* occupied the separate niche. This species formed the communities in very shallow marginal zones of lakes (0.4–1.5 m) with other macrophytes like: *Chara vulgaris, C. tomentosa, Potamogeton ´ nitens*, and monospecific stands on margins of steep lake slopes (4–6 m) with *Chara globularis fo. hedwigii* and *Nitella mucronata*.

The process of extinction of this species seems to be related with increasing turbidity related in turn to algal blooming in lakes and with the spatial competition of vascular macrophytes, especially *Ceratophyllum demersum*.

KEY WORDS: *Lychnothamnus barbatus,* charophytes, distribution, water chemistry, aquatic vegetation, environmental niche, endangered species.

1. INTRODUCTION

Lychnotamnus barbatus (Meyen) Leonhardi 1863 a representative of the monotypic genus *Lychnotamnus*, belongs to the rarest charophytes in the world (McCourt *et. al.* 1999, Casanova *et al.* 2003, Chou *et al.* 2007). According to the fossil evidence, *L.*

barbatus was widespread in the world from late Eocene to Holocene. It was also widespread in Pliocene, however, after this period the decline of this species was noted (Soulie-Märsche 1989, Casanova *et al.* 2003, García 2003). Presently, there is a small number of its stands within the disjunctive range (Karczmarz 1967, Blaženčić and Blaženčić 1983, Krause 1986, Casanova *et al.* 2003, Chou *et al.* 2007). It occurs mainly in Central and Southern Europe (Poland, Lithuania, Germany, Austria, France, Italy, Croatia, Slovenia and Romania) and in the River Volga valley (eg. Mowszowicz 1947, Corillion 1957, Karczmarz 1967, Blaženčić and Blaženčić 1983, Hollerbach and Krasavina 1983, Golub *et al.* 1991, Krause 1997, Balevičius 2001, Blaženčić *et al.* 2006). It has been reported also from Asia and Australia (India, China, Papua New Guinea, Taiwan and Australia) (e.g. Chatterjee 1970, McCourt *et. al.* 1999, Casanova *et al.* 2003, Garsia 2003, Chou *et al.* 2007). A review of its stands in the world is given in the papers by Wood (1964) and Casanova *et al.* (2003). Krause (1997) reported that the centre of the European range of this rare species of Characeae is in Brandenburg in Germany and in Poland.

In the last decade in Europe a decline of *L. barbatus* has been noted (Krause 1997, Blažencić *et al.* 2006, Casanova *et al.* 2003). This species is considered as the one of the charophyte species the most threatened in Europe (Balevičius and Ladyga 1992, Schmidt *et al.* 1999, Kusber *et al.* 2006, Blaženčić and Blaženčić 2003, Blaženčić *et al.* 2006, Siemińska *et al.* 2006). There is no reports in the published sources of *L. barbatus* spontaneous development from the new stands (Krause 1997).

Lychnothamnus barbatus has been reported in Poland from a number of localities since the middle of the 19th century (Klinggräff 1884, Abromeit 1884, Karpiński 1938). This charophyte species is one of the most rarely noted species of *Characeae* (Dąmbska 1964, 1966, Gąbka 2006). *L. barbatus* is legally protected and is listed in the category E (endangered) on the *Red list of threatened algae in Poland* (Siemińska *et al.* 2006). Although the distribution of *L. barbatus* has been of interest to many authors, little is known about ecology of this species in Central Europe and about the reasons for its decline.

Results of the earlier studies of *L. barbatus* permitted formulation of two working hypotheses to be tested: 1) the distinct character of localities where *L. barbatus* occurs is defined by chemical and physical parameters of water and the range of depth and the gradient of light accessibility related to depth and turbidity, 2) development of vascular vegetation and eutrophic species of charophytes has substantial restricting effect on the abundance and distribution of *L. barbatus* in lake littoral.

The main aims of this work were to determine a) the abundance of *L. barbatus* and co-occurring species at different sites in lakes, b) the most important ecological parameters controlling the vegetation structure of *L. barbatus* communities and quantitative responses of *L. barbatus*.

The paper presents a review of all known localities of *L. barbatus* in Wielkopolska region and south Pomerania region in Western Poland, including their past and present distribution.

2. STUDY SITES

The study was performed in western Poland in Wielkopolska Lakeland and south Pomeranian Lakeland (Fig. 1) – the region of last Vistulan glaciation. Overall extent of the study area was close to 30,000 km^2. The lakes' water of this region is mostly alkaline and containing large amounts of Ca^{2+}. The lakes are mostly shallow, of eutrophic type and they occur in agricultural landscape (Choiński 1995, Burchardt 1996).

Lychnothamnus barbatus was found mostly in lakes rather large, from 5.5 to 197 ha, deep and/or very deep (maximal depth 7.8–38 m). Usually the lakes have steep slopes of basins and narrow shallow zone, while the mean depth of the lakes was relatively great (over 4.5 m). The field work was conducted during the vegetation period (July–September), in the years 2005–2007. Over this period the earlier reported sites of *L. barbatus* were verified and new sites were found.

The distribution of *L. barbatus* in study area was based upon three types of data: the herbarium collections (the Professor I.

Dąmbska Charophyta Herbarium, placed in Department of Hydrobiology, Adam Mickiewicz University) gathered mostly between 1840–2005, published data and the data of this study.

Materials documenting the newly found sites were deposited in the Charophyta Herbarium of the Department of Hydrobiology, Adam Mickiewicz University in Poznań.

3. METHODS

The distribution and abundance analysis of *Lychnothamnus barbatus* was made on the basis of 9 vegetation sample plots of 16 m^2 from different sites in 4 lakes. The Braun-Blanquet method (Dierschke 1994) for vegetation records was used for estimation the species cover in the field and the values were transformed into point scale according to van der Maarel (1979). The 14 sites (located in 3 lakes) of this species occurrence known from published papers (Dąmbska 1961, 1966, Gołdyn 1983) were included.

The area of the vegetation plots from literature data was variable (16–100 m^2). The vegetation analysis was conducted in the lakes (Fig. 1) where sites (or groups of sites) with the *L. barbatus* were designated (in brackets – number of plots): Lake Brzostek (5), Lake Lubosz Wielki (2), Lake Gorzyckie (1), Lake Tuczno (1), Lakie Muchocińskie (1, Dąmbska 1961), Lake Gorzyńskie (1, Dąmbska 1961) and Lake Kuźnickie (12, Gołdyn 1983).

The floristic composition under study was presented in one synthetic table of shortened form (Table 1). Abundance, constancy and coefficient of cover were assessed. *Abundance* was determined according to a six-degree scale developed by Braun-Blanquet (Dierschke 1994). *Constancy* was determined according to the following scale: V – species occurring in 80–100% of vegetation records; IV – species present in 60–80% records; III – species present in 40–60% records; II – species present in 20–40% records; I – species present in 10–20% records; + – species present in 5–10% records and r – species occurring in 0–5% records.

Charophyte names are those used by Krause (1997), vascular plants' names – by Mirek *et al.* (2002), and names of mosses followed Ochyra *et al.* (2003).

Table 1. Synoptic table of 23 vegetation records with *Lychnothamnus barbatus* from lakes of Wielkopolska Region (Western Poland). Abundance: according to six degree scale of Braun-Blanquet (modified), Constancy: according to I–V scale of % frequency in 23 records (see Methods for details).

Species	Abundance							Constancy	
	5	4	3	2	1	+	r		
Lychnothamnus barbatus (Meyen) Leonhardi	9	2	1	1	3	7	•	V	100%
Ch. *Charetea fragilis*:									
Nitellopsis obtusa (Desvaux) J.Groves	•	•	2	1	4	1	•	II	35%
Chara globularis fo. *Hedwigii* Agardh	•	•	•	•	2	1	•	I	13%
Chara globularis Thuillier	•	•	•	•	•	2	•	+	9%
Chara tomentosa Linné	•	1	•	•	1	•	•	+	9%
Chara vulgaris Linné	•	•	•	•	1	•	•	r	4%
Nitella mucronata (A.Braun) Miquel	•	•	•	•	•	1	•	r	4%
Ch. *Potametea*:									
Ceratophyllum demersum L.	4	5	1	1	4	3	•	IV	78%
Myriophyllum spicatum L.	•	•	•	•	2	4	•	II	26%
Najas marina L.	•	•	•	•	1	2	•	I	13%
Elodea canadensis Michx	•	•	1	1	•	•	•	+	9%
Potamogeton × *nitens* Weber	•	•	•	•	•	1	•	r	4%
Potamogeton friesii Rupr.	•	•	•	•	•	1	•	r	4%
Ch. *Fontinaletea*:									
Fontinalis antipyretica L.	•	•	•	2	3	2	•	II	30%

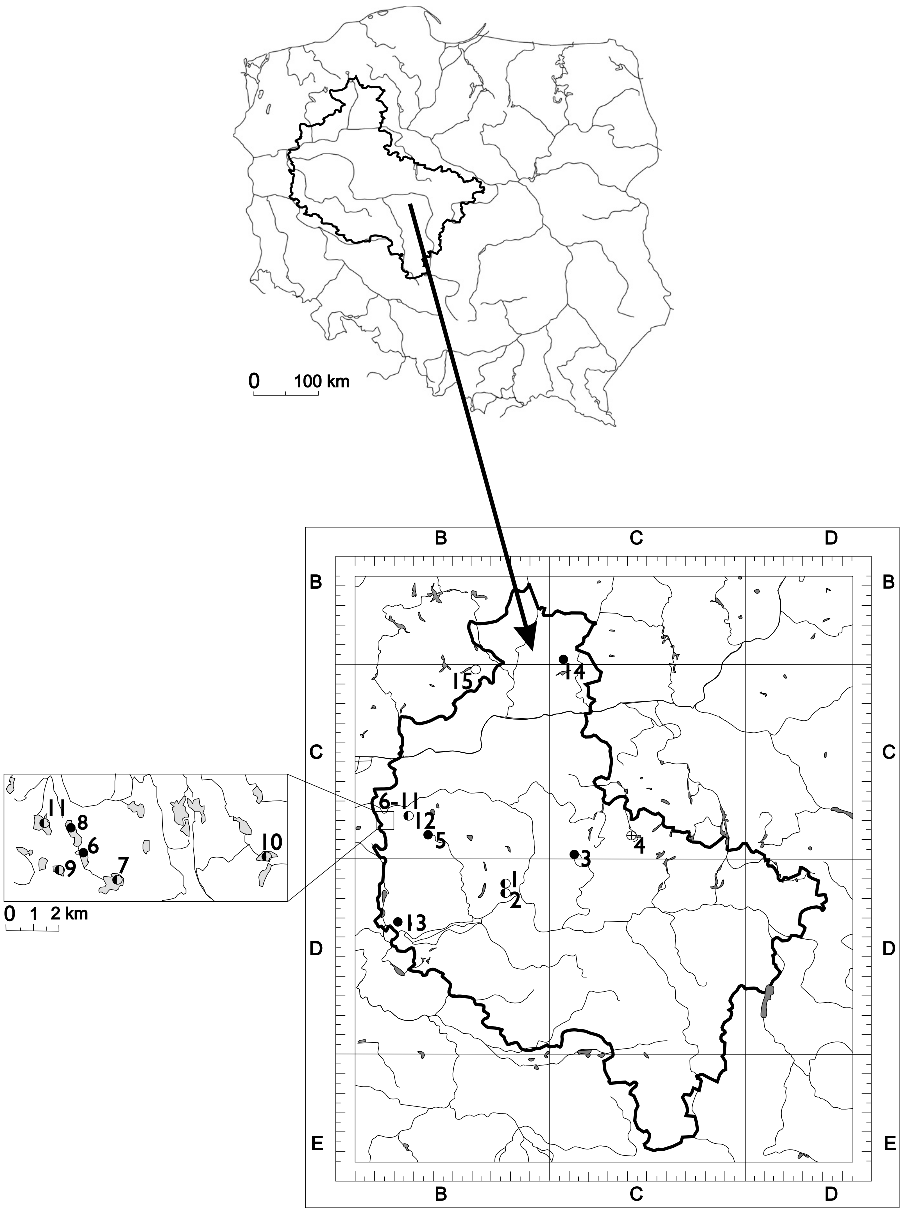

Fig. 1. The distribution of *Lychnothamnus barbatus* in 15 lakes of Wielkopolska region, (Western Poland) using the ATPOL grid square system (5 × 5 km).
Sites: before period 1990 (○), 1900–1944 (⊕), 1945–1979 (◐), after period 1980 (●).
Locations: 1. Lake Góreckie near Poznań (collected by Dąmbska in 1949 and by Sieminiak in 1970); 2 Lake Jarosławieckie near Poznań (collected by Dąmbska in 1949); 3. Lake Brzostek near Pobiedziska (collected by Gąbka in 2006); 4. Lake Jankowskie near Jankowo Dolne (collected by Karpiński in 1935); 5. Lake Lubosz Wielki (Dobrzyczno) near Lubosz (collected by Gąbka and Owsianny in 2006); 6. Lake Gorzyckie (Wiejskie) near Gorzycko (collected by Dąmbska in 1951 and by Gąbka and Owsianny in 2007); 7. Lake Gorzyńskie near Gorzycko (collected by Dąmbska in 1951); 8. Lake Tuczno near Gorzycko (collected by Dąmbska in 1951 and by Gąbka, Owsianny in 2007); 9. Lake Wielkie near Gorzycko (collected by Dąmbska in 1958); 10. Lake Młyńskie near Międzychód (collected by Dąmbska in 1951); 11. Lake Winnogórskie (Muchocińskie) (Dąmbska 1961); 12. Lake Janukowo near Sieraków (collected by Dąmbska in 1952); 13. Lake Kuźnickie near Grodzisk Wiekopolski (collected by Gołdyn in 1981); 14 lake Borówno (Borówie) near Kujan (Abromeit 1884 and collected by Owsianny in 2006); 15. Lake Chmiel Mały (Kl. Kameelsee) near Wałcz (collected by Caspary and in Klinggraeff 1881, Abromeit 1884, Migula 1897).

Three water samples were taken in the central part of sample plot with *Lychnothamnus barbatus* occuring from 4 lakes (Lake Brzostek, Lake Lubosz Wielki, Lake Gorzyckie, Lake Tuczno) in 2006–2007. They were poured into plastic containers, two of which were immediately preserved: one with 1 ml of concentrated nitric acid, the other with 1 ml of 95% chloroform. The last sample was not preserved. The following parameters were measured in the field: pH, water temperature, conductivity, dissolved oxygen and oxygen saturation. The remaining ones were measured in laboratory. Physical and chemical analyses were performed according to standard methods for hydrochemical analyses (Hermanowicz *et al.* 1999). 19 water parameters were analysed: colour, acidity (pH), conductivity, O_2 dissolved and saturation, NH_4^+, NO_3^-, PO_4^{3-}, SO_4^{2-}, Ca^{2+}, Mg^{2+}, Na^+, K^+, total Fe and chlorophyll *a* concentration. Water samples for color analyses were filtered through 0.45 μm membrane filters. The depth ranges at the sites of *L. barbatus* occurrence were determined.

CANOCO software (ter Braak and Šmilauer 1998) was used for multivariate analyses. For the exploration of main variables governing plant species distribution we applied the detrended correspondence analysis DCA (ter Braak and Šmilauer 1998). Our data showed large beta-diversity (wide gradient), therefore we assumed that applied ordination methods will give the reliable results Otypková and Chytry (2006).

Lychnothamnus barbatus and co-occurrence species response curves to maximal depth of water were modeled by GAMs model (generalized additive models, Hastie and Tibshirani 1990). We using Poisson distribution and smooth term complexity was selected using the Akaike information criterion (Lepš and Šmilauer 2003).

4. RESULTS

4.1. Records of *Lychnothamnus barbatus* in Western Poland

According to the herbarial materials and published or not published reports in Wielkopolska region, Western Poland (Fig. 1) there are 15 known sites of *Lychnothamnus barbatus*. The first information on the presence of this species comes from the northern part of the region and was published by Abromeit (1884) and Klinggräff (1884) in the second half of the 19th century (Fig. 1, no. 14, 15). In the period between the two world wars one site of this species was found near Gniezno (Karpiński 1938, herbarial materials).

Much information on *L. barbatus* was provided by herbarial materials from the collection of Prof. Izabela Dąmbska deposited at the Hydrobiology Department, Adam Mickiewicz University, Poznań. The majority of *L. barbatus* sites were found in the second half of the 20th century (Dąmbska 1952, 1961, Gołdyn 1983). In 2006 the authors of this paper found new sites of this species in Lake Brzostek and Lake Lubosz Wielki (Dobrzyczne) (Fig. 1, no 3, 5). In the years 2005–2007, all earlier specified stands of the species were verified and the presence of this species in the three lakes: L. Gorzyckie, L. Tuczno and L. Borówno (or L. Borówie) was confirmed (Fig. 1, no. 6, 8, 14). In total, in the Wielkopolska region, this species was found at 15 sites (Fig. 1). The most abundantly *L. barbatus* was found in the Międzychodzko-Sierakowskie Lake District (8 sites; Fig. 1, no. 5–12). The distribution of all past and present localities of *L. barbatus* is presented in Fig 1.

In the lakes of the Wielkopolska region *L. barbatus* was usually noted in low numbers, most often this species was represented by individual plants. As follows from published data and our own study, only in Lakes Gorzyńskie (Dąmbska 1961) Kuźnickie (Gołdyn 1983) and Lubosz Wielki (our research; Fig. 1, no. 7, 13, 5) large populations of this species were found, assembled in one part of the lake. The majority of sites of *L. barbatus* were localised at shallow sites or at the margins of the lake beaches or at the sites used earlier as watering places for livestock. Particularly interesting is the presence of a very abundant population of this species in Lake Brzostek (Fig. 1, no. 3) in which *L. barbatus* grew in large patches and was the dominant species in the lake littoral.

4.2. Vegetation composition and habitat vertical gradients

Quantitative data on *Lychnothamnus barbatus* and the information on the co-occurring plant species from the study plots were

Table 2. Depth of water, Secchi disc visibility (SD), physical and chemical properties of water found in six habitats of *Lychnothamnus barbatus* (n = 6) of four lakes (Fig. 1, no. 3, 5, 6, 8) .

Property	Unit	Range	Mean
Depth of water	m	1.5–3.4	2.07
Secchi disc visibility	m	1.5–3.5	2.07
Chlorophyll *a*	μg cha l^{-1}	5.05–13.63	9.05
Colour	mg Pt l^{-1}	2–10	6.17
pH		7.91–8.08	8.01
O_2 dissolved	mg O_2 l^{-1}	71.3–151.5	102.04
Saturation	%	5.87–12	9.12
Conductivity	μS cm^{-1}	293.4–567.9	440.85
$N\text{-}NH_4^+$	mg N l^{-1}	0.01–0.26	0.10
$N\text{-}NO_3^-$	mg N l^{-1}	0–0.04	0.01
$P\text{-}PO_4^{3-}$	mg P l^{-1}	0.02–0.16	0.05
Total Fe	mg Fe l^{-1}	0.03–0.25	0.08
Ca^{2+}	mg Ca l^{-1}	43.5–74.4	61.87
Mg^{2+}	mg Mg l^{-1}	5.5–14.26	10.55
Na^+	mg Na l^{-1}	9.1–19.45	11.53
K^+	mg K l^{-1}	3.1–18.88	6.82
SO_4^{2-}	mg SO_4 l^{-1}	20–80	53.50

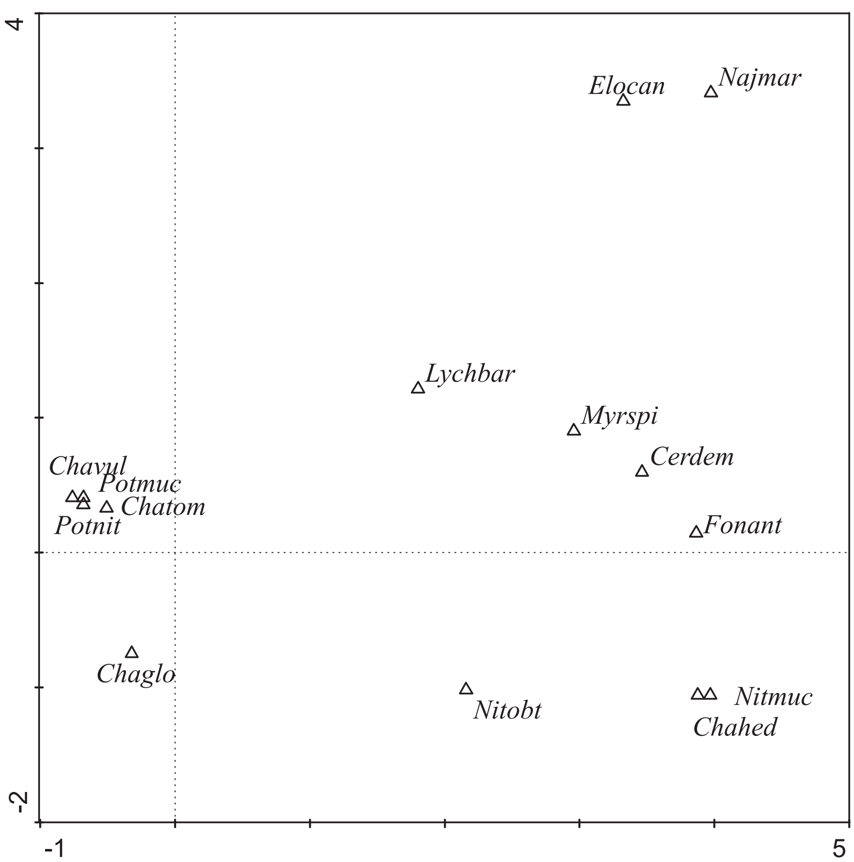

Fig. 2. Detrended correspondence analysis for species optima along the first two axes. Species list: Lychbar – *Lychnothamnus barbatus*; Nitobt – *Nitellopsis obtusa*; Chahed – *Chara globularis fo. hedwigii*; Chaglo – *Chara globularis*; Chatom – *Chara tomentosa*; Chavul – *Chara vulgaris*; Nitmuc – *Nitella mucronata*; Cerdem – *Ceratophyllum demersum*; Myrspi – *Myriophyllum spicatum*; Najmar – *Najas marina*; Elocan – *Elodea canadensis*; Potnit – *Potamogeton × nitens*; Potmuc – *Potamogeton friesii*; Fonant – *Fontinalis antipyretica*.

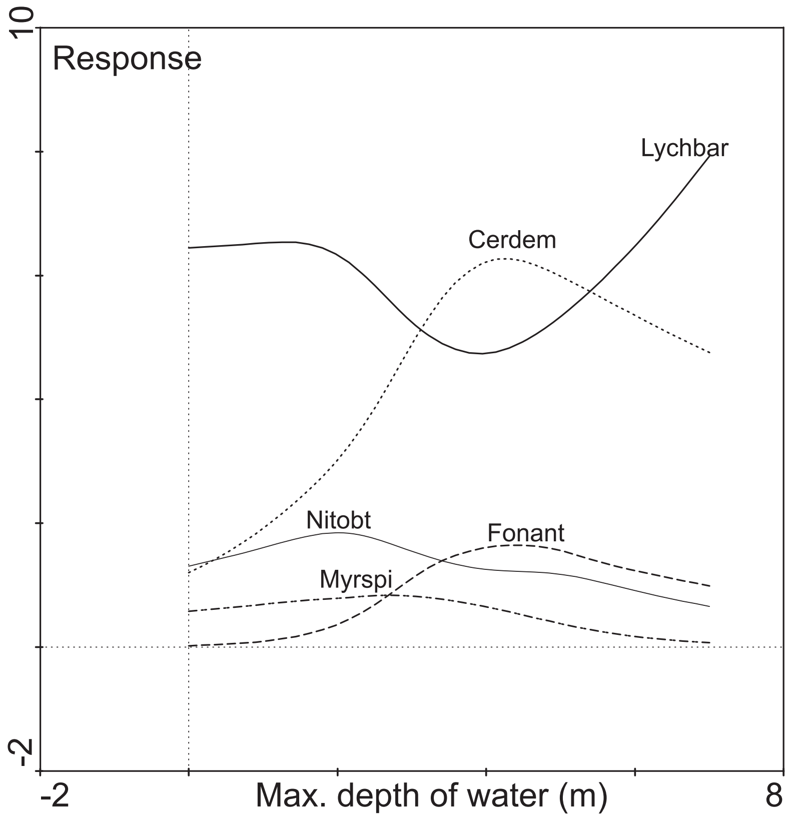

Fig. 3. *Lychnothamnus barbatus* (Lychbar) and *Ceratophyllum demersum* (Cerdem) response curves to the maximal depth of water gradient modelled by the Generalized Additive Model using Poisson distribution smooth term complexity selected according to AIC criterion. The first axis represents the maximum depth of water values and the second axis represents the cover codes in the van der Maarel scale. Species list: Nitobt – *Nitellopsis obtusa*, Myrspi – *Myriophyllum spicatum* and Fonant – *Fontinalis antipyretica*.

collected from 7 lakes (Fig. 1, no. 3, 5–8, 11, 13) listed in Table 1. The sites analysed were poor in species (5 charophytes, 6 vascular plants and 1 bryophytes). The cases where *L. barbatus* was dominating or abundant were very rare. At the sites with *L. barbatus* the total number of other species were noted, on average there were 3 plant species accompanying *L. barbatus*. Only at 9 sites the abundance of *L. barbatus* was significant. The most often accompanying species was *Ceratophyllum demersum*, which occurred in considerable numbers. Out of the 12 species co-occurred with *L. barbatus*, only *Myriophyllum spicatum, Nitellopsis obtusa* and *Fontinalis antipyretica* reached the II degree of constancy.

The sites with *Lychnothamnus barbatus* were arranged according to species composition and their occurrence along the two DCA axes (Fig. 2). The study plots with *L. barbatus* showed a wide spectrum of species ranging from characteristic of poor and rich water, being a complex of transitions between shallow and deep sites. The diversity of vegetation was related to the single dominant gradient determined by the length of the first DCA axis (4.30).

Axis 1 shows the depth gradient – from shallow sites with species like. *Chara vulgaris*, *C. tomentosa*, *Potamogeton* × *nitens* and *P. friesii*, to deep ones with. *Chara globularis* fo. *Hedwigii* and *Nitella mucronata*. The axis 2 can be interpreted in terms of trophic requirements of the particular species: from charophyte species (e.g. *Nitellopsis obtusa*, *Nitella mucronata* and *Chara globularis*) to eutrophic species (*Najas marina* or *Elodea canadensis*).

We tested the correlation between three main axes resulting from DCA and depth of water (Pearson coefficient: axis 1 r = 0.74, axis 2 r = 0.25, axis 3 r = –0.11). Strong positive correlation exists between variables and the first axis that represents a depth gradient. However, it is probably also connected with light conditions gradient that was not measured in all cases.

4.3. Depth gradient and water chemistry

The relations between the species composition of the sites with *Lychnothamnus barbatus* and the maximum depth of water were analysed. In particular the analysis was made of the 4 accompanying species of the greatest frequency of occurrence at the sites with *L. barbatus*. Quantitative response curves of the *L. barbatus* and the most common species at a given depth of water reveal differences (Fig. 3). Taking into regard the depth of water at which it occurred, *L. barbatus* occupied a distinct niche in the studied lakes. It reached the optimum condition in very shallow water (up to 1.5 m) but occurred in great abundances in very deep sites (deeper than 5 m). In contrast, the optimum occurrence of *Ceratophyllum demersum* was related to the depth in the range 2–4 m. In shallow and deep water (the sites occupied by *L. barbatus*) *C. demersum* reached low abundance. It should be mentioned that this species was the most frequent species accompanying of *L. barbatus*.

The accompanying species of lower abundance *Nitellopsis obtusa* and *Myriophyllum spicatum* reached greater frequency at the shallow sites, up to 3 m, whereas the greatest contribution of *Fontinalis antipyretica* was found at the depth of 3–4 m. The depth of water at the sites with *L. barbatus* varied from 0.5 to 6 m (3.5 m on average). The physical and chemical parameters of water were analysed in detail at 6 selected sites of *L. barbatus* occurrence. Usually *L. barbatus* was found at the sites of greater Secchi disc visibility, basic pH of water, rich in Ca^{2+}, Mg^{2+} and SO_4^{2-} and high content of NH_4^+ and PO_4^{3-} and an moderate degree of conductivity (Table 2). The contents of the nutrients changed in wide ranges. The water was poor in NO^{3-}, Na^+, K^+ and total Fe. At the sites with *L. barbatus* the water was strongly oxydated. The concentration of chlorophyll was rather low. In general, the sites with *L. barbatus* occurred in meso- and moderate eutrophic waters. This species was found on the substrate of calcareous gytja or fine-grain mineral substrates with a small contribution of organic matter.

5. DISCUSSION

5.1. Water chemistry and floristic diversity of sites with *Lychnothamnus barbatus*

Lychnothamnus barbatus belongs to the rarest and strongly threatened with extinction representatives of *Characeae* in Western Poland. As follows from the information collected in Casanova *et al.* 2003, *L. barbatus* occurs most often in lakes and rarer in ponds, rivers or marshy areas. In Wielkopolska region, (Western Poland) this species has been observed in lakes but in Poland there is the evidence proving its occurrence in running waters (Torka 1908).

According to many authors the ecological tolerance if *L. barbatus* is narrow (Karczmarz 1967, Krause 1981, Blaženčić and Blaženčić 1983, Balevičius 2001, Chou *et al.* 2007). Casanova *et al.* (2003) put forward a hypothesis that *L. barbatus* does not tolerate low accessibility of light and increased trophic state of water. It should be regarded however, that the earlier publication on this species gives very scarcely the habitat details. In Germany and Austria *L. barbatus* grew in post-glacial lakes of water poor in nutrient substances and strongly oligosaprobic (Corillion 1957, Krause 1986, 1997).

At the majority of localities in Central Europe (Germany, Austria, Lithuania) this species was noted at the sites of considerable depth and good water transparency. In Croatia this species was most often found in shallow zones of mesotrophic lakes (Blaženčić and Blaženčić 1983, Blaženčić and Blaženčić 2002). In oligotrophic -eutrophic lakes of Lithuania this species is considered as a suitable indicator of low lake trophic state (Balevičius 2001, Balevičienė and Balevičius 2006). In Central Europe *L. barbatus* grows in lakes of high content of Ca in water from limestone rich area (Karczmarz 1967, Krause 1981, 1986, Balevičius 2001). The pH of waters at the majority of *L. barbatus* sites in Europe was alkaline, only the water in Lake Šipak in Croatia this species occurred at slightly acidic or neutral pH (Blaženčić and Blaženčić 1983). Detailed ecological study of this species in Australia has proved that it grows at shallow sites of clear, non-turbid alkaline water of good transparency and different conductivity (240–410 µS cm^{-1}) (Casanova *at al.* 2003).

In the studied lakes of Wielkopolska region in Western Poland, *Lychnothamnus barbatus* occurred in hard water, relatively rich in Ca^+ (mean±SD = 61.9±12.7 mg Ca l^{-1}) and decidedly alkaline pH (pH 8.01±0.07), poor in the bioavailable forms of nutrient substances, in particular N-NH_4^+ (0.1±0.09 mg N l^{-1}) and P-PO_4^{3-} (0.05±0.06 mg P l^{-1}), and of high conductivity (440.8 ±117.5 µS cm^{-1}). A significant habitat feature of this charophyte species is usually low chlorophyll a (phytoplankton biomass) concentration (9.05±3.5 µg Chl *a* l^{-1}) and higher Secchi disc depth (2.07±0.64); these two factors indicate that the turbidity and low light attenuation are probably decisive for *L. barbatus* occurrence.

Earlier studies have shown relatively high species richnes at the sites with *L. barbatus* in Central Europe. In the lakes of Lithuania this species occurred in total with 22 species of macrophytes, including 5 species of charophytes (Balevičius 2001). It occurred most frequency in company of *Chara tomentosa* and *Fontinalis antipyretica*. In Lake Šipak in Croatia it occurred together with *Chara hispida*, and vascular plants e.g. *Potamogeton* spp. *Myriophyllum spicatum* and *Ceratophyllum demersum* (Blaženčić and Blaženčić 1983). In Germany, *L. barbatus* was mainly found in communities with *Nitellopsis obtusa* (Krause 1981, 1986). Its co-occurrence with the latter species was also reported from Poland (Karczmarz 1967, Karczmarz and Krause 1979, Pełechaty and Pukacz 2005). At the 23 vegetation records from Wielkopolska region, the total number of 12 species was found in eutrophic lakes in which *L. barbatus* often appeared in associations with *Ceratopyllum demersum*. However, it was also recorded together with *Nitellopsis obtusa* and *Potamogeton* species, which indicated the mesotrophic conditions.

It seems that particularly important factors in the ecology of *L. barbatus* include the depth of water and local light conditions, mutual spatial relations with vascular plants and other species of charophytes. Of interest is the specificity of the ecological niche of *L. barbatus* against those of the other macrophyte species in the studied lakes. Taking into regard the gradient of depth of *L. barbatus* occurrence, the sites of its greatest contribution and compactness were found near the shore beaches and sites earlier used as watering places for livestock; there are the sites where the growth of vascular plants was restricted by mechanical damage. On the other hand, *L. barbatus* was abundant at the sites in deep water, inaccessible for the vascular plants, especially for *Ceratophyllum demersum*, because of lower tolerance of this species to poor light conditions. It should be emphasised that *L. barbatus* occupies deeper layers only in water of high transparency. At these sites it grows on the steep slopes of the lake basins. The contribution of *L. barbatus* was the lowest at intermediate depth, most often taken by other macrophytes.

It seems that the depth of water was identified as the one factor influencing the plant species composition of the sites with *L. barbatus*, while another important factor was the access of light. The distinct character of the niche of this species along the gradient of depth was affected by the development of vascular plants, especially eutrophic species.

5.2. Decline of *Lychnothamnus barbatus* – effect of trophic changes of lakes or influence of co-occurring vascular vegetation?

Lychnothamnus barbatus is probably a very important indicator of trophic changes in the lakes and its decline is related to serious transformations in the lake littoral vegetation. In the last decade of the 20th century, *L. barbatus* withdrew from the earlier occupied sites in many regions of the world (Krause 1997, Casanova *et al.* 2003). In Poland, recently *L. barbatus* has been sporadically noted (e.g. Sugier *at al.* 2008). The main reason for its decline in Europe – so also in Poland – is increasing trophic state of waters, in particular decreasing transparency of water being a consequence of mass development of phytoplankton (Karczmarz 1967, Krause 1997, Casanova *et al.* 2003). As proved by Karczmarz (1967) *L. barbatus* is able to reach its maximum growth and full developmental cycle only in the conditions of high transparency. The decrease in water transparency, and increase of its turbidity – is the main factor restricting generative reproduction of this species (Karczmarz 1967). Similar conclusions can be drawn on the basis of the results obtained for the lakes in studied Wielkopolska region. Only in 4 lakes the recent occurrence of the species confirmed the earlier reports. The disappearance of the species was mainly a consequence of deterioration of the light accessibility and increasing trophic state of the lakes (Gąbka and Owsianny, unpubl.). The assemblages of planktonic algae of lakes with sites of *L. barabtus* were typical for eutrophic and alkaline waters like; Dinoflagellata: *Peridiniopsis polonicum* (Woloszynska) Bourrelly, *P. cunninghtonii* Lemmermann, *P. berolinense* (Lemmermann) Bourrelly, *P. elpatiewskyi* (Ostenfeld) Bourrelly, *Ceratium hirundinella* (O.F. Müller) Dujardin, *Gonyaulax apiculata* (Penard) Entz, *Kolkwitziella acuta* (Apstein) Elbrächter; Owsianny unpubl.).

On the other hand, *L. barbatus* withdraws because its habitats are taken by morphologically and ecologically similar species, mainly other charophytes (Casanova *et al.* 2003). As proved in experimental study, *L. barbatus* forms a small number of oospores and unstable bank of oospores (Casanova *et al.* 2003). Its main mode of reproduction is vegetative and it has poor competitive abilities. Hence, highly likely is the hypothesis put forward by Casanova *et al.* (2003) that this species has very low possibility to return generatively to the sites from which it has once withdrawn even after habitat conditions have changed in advantage for the species. In regard to the above it is important to discern if the disappearance of *L. barbatus* in Wielkopolska region is a result of the environmental changes or the colonisation by other species of charophytes or vascular plants of similar habitat demands. As follows from our studies, this species occupies in lakes a distinct niche along the depth gradient. Poor reproduction abilities and the occurrence at significant depths make this species particularly sensitive to changes in local light conditions.

The responses of *Lychnothamnus barbatus* and *Ceratopyllum demersum* to the depth gradient clearly illustrate the differences in their niches. Dominance of *C. demersum* is intriguing and suggests that it should have very wide ecological tolerance occurring in such diverse habitats. *C. demersum* should be treated as ecologically similar to *L. barbatus* because of its attraction to waters rich in calcium and of high trophic state (Kłosowski 2006). As we suppose, one of the reasons for disappearance and quantitative changes in *L. barbatus* occurrence in the lakes studied is the competitive exclusion by *C. demersum*. It is generally regarded as invasive species and causing a decrease in the biodiversity of lakes, especially of eutrophic shallow lakes in Wielkopolska region (Gąbka unpublished). Our results have shown that *C. demersum* is abundant in the lakes in which *L. barbatus* is present and *C. demersum* is an important component of vegetation in the lakes in which the presence of *L. barbatus* was earlier reported and currently not found.

In some lakes *Nitellopsis obtusa* may play a similar role. It is a large-size species of similar habitat demands and it often accompanies *L. barbatus*.

Agricultural land use affects the environment of the lakes in Wielkopolska region (Burchardt 1996). Our supposition is that the decline of *L. barbatus* in lakes is a result of the narrow ecological optimum of this taxon and the processes connected with human impact (drainage and eutrophication) as well as with invasion of eutrophic species of macrophytes. In the 1970–1990 when the majority of the earlier known localities of *L. barbatus* in Poland disappeared, the main reasons of this disappearance include the agricultural use of the catchment area and intense fertilisation of the land with mineral fertilisers and untreated sewage management. After 1989, the political and economical changes in Central Europe brought at first crisis in agricultural production followed by an increase in the level of ecological awareness and the main reasons for the further decline of *L. barbatus* included the invasion of macrophytes in lakes of increasing trophic state, decrease in the water table and disturbances of fish distribution in lakes contributing to increasing eutrophication.

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