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EFFECT OF ENVIRONMENTAL CONDITIONS ON THE POPULATIONS OF *LURONIUM NATANS* (L.) RAF.

ABSTRACT: The structure (aggregations` distribution, density, age structure) of *Luronium natans* L. (Raf.) populations has been studied in 21 lakes in the Pomeranian Lakeland (NW Poland), where the highest population density of this species is found in slightly acid (pH 6–7) waters, poor in DOC (<6.0 mg C dm^{-3}) and phosphorus (<30.0 μg TP dm^{-3}). *Luronium natans* reproduces mainly vegetatively and prefers shallow (1–2 m), mineral-organic (5.1–10.0% C) substrates. Seedlings represent about 10% of a population. High levels of pH (pH>8.0), concentration of carbon (>6.0 mg C dm^{-3}) and phosphorus (>30.0 μg TP dm^{-3}) impede the population growth. Under such conditions population density may be lower by as much as 80–90%, aggregation size smaller, and the proportion of generative stems higher. *Luronium natans* aggregation size depends on the depth: the deeper the location – the larger and denser the aggregation, the shallower the location – the larger the fraction of generative individuals (up to 98% of the population).

KEY WORDS: *Luronium natans*, age structure, density, submerged macrophytes

1. INTRODUCTION

Luronium natans (L.) Raf. (Alismataceae) is an evergreen clonal species with an iterative growth type. In the submerged sites this plant forms a rosette of narrow and delicate leaves, and in summer, additionally, floating leaves with long petioles (Casper and Krausch 1980, Rich and Jermy 1998). *Luronium natans* reproduces primarily vegetatively by propagules, owing to which it can colonize unoccupied spaces (Harper 1977, Barrat-Segretain and Amoros 1996, Barrat-Segretain *et al.* 1998, Falińska 2002). Some propagules, suspended in the water bulk, may colonize the new areas (Willby and Eaton 1993, Greulich and Bornette 1999). Vegetative propagation, heavy seeds and evergrenness favour the formation of aggregations (Van Groenendael and de Kroon 1990, Van Groenendael *et al.* 1996, Greulich *et al.* 2000). Growing in an aggregation offers a greater chance to survive and dominate in the competition with other species for the resources of the habitat (Zarzycki 1965, Symonides 1979) and makes the use of available resources more efficient. In clonal plants it is affected by a transfer of assimilates (Alpert and Mooney 1986, Jonsdottir and Callaghan 1990, Alpert 1991, Steufer *et al.* 1994, Jonsdottir and Watson 1997). This character is particularly advantageous in conditions unfavourable for plant growth (Steufer *et al.* 1996, Price and Marshal 1999). It has been demonstrated that dense plant populations occupying large areas are less threatened by extinction than ones that are small and not very numerous (Fischcer and Matthies 1998, Kéry *et al.* 2000). In the case of *Luronium natans*, it seems significant to assess the environmental conditions on which the aggregation size depends.

Aquatic environment heterogeneity is one of the factors which diversifies the structure of a population and determines its fate (Szmeja 1992). As a rule, populations found in low-productive habitats are characterized by a high density (Szmeja 1994, Coops *et al.* 1996). Mature individuals are then small, but numerous, due to which they have a better chance to survive in a given site. In turn, populations found in nutrient-rich habitats are less numerous, conspecific adult individuals are larger and more fecund, and thereby the probability of their survival is greater (Szmeja 1987a, 1994).

Population structure depends among other things on the genetic characters of a species, biotic and intrapopulation interactions and environmental conditions (Falińska 2002). Age composition in a population is a good material for forecasting the fate of population (Andrzejewski and Falińska 1986). An analysis of age composition indicates that in progressive populations the juwenile and reproductive individuals are numerous, whereas in regressive populations the senile and postgenerative individuals prevail. It was therefore decided to study the age structure of vanishing *Luronium natans* populations. The environment determines this structure in two ways: by eliminating individuals at a specified age, or by a temporary limitation of reproduction. Population endurance is best sustained by the fraction, numerous every year, of seedlings and generative individuals (Szmeja 1992, Falińska 2002). From the point of view of *Luronium natans* protection, it is worthwhile to assess also this population characteristic. Therefore it is the aim of the study to determine the kind and range of changes in the structural features of *Luronium natans* populations under the influence of such environmental factors as: pH, phosphorus and organic carbon concentrations in the water and organic matter in the sediment, as well as age structure of individuals.

2. MATERIAL AND METHODS

The studies were carried out in the vegetation season July 2001 and 2002 in 21 lakes in the Pomeranian Lakeland (NW Poland; Fig. 1) Plant samples 0.1 m^2 in size were collected from aggregations of typical density in the middle of the population areas. The samples, 3 from each lake, were used for counting the ramets and classifying them according to developmental stages. The unit used in the subsequent analyses of numbers, density and age distribution was the stem (ramet). Additionally, over a 150 m shoreline stretch of each lake *Luronium natans* aggregations were counted and their length and breadth were measured. Aggregation area was calculated by the formula used for the computation of ellipse area.

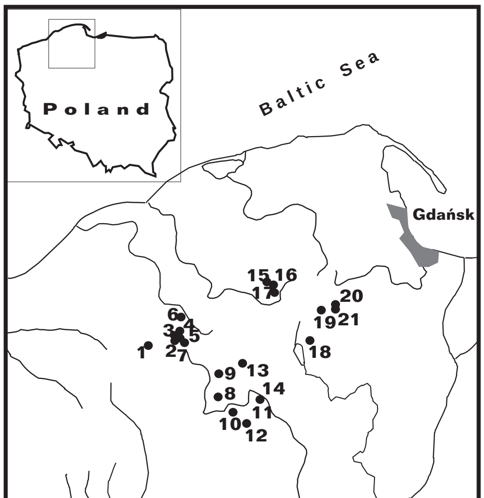

Fig. 1. Location of the lakes under study (1–21) in Pomeranian Region (North-West Poland). 1. Bobięcińskie, 2. Orle, 3. Kamień, 4. Smołowe, 5. Dolskie, 6. Święte, 7. Piasek, 8. Liny, 9. Krasne, 10. Linowskie, 11. Sporacz, 12. Okoń, 13. Nowoparszczenickie, 14. Moczadło, 15. Ostrowite, 16. Warleńskie, 17. Baroczno, 18. Drzędno, 19. Świniebudy, 20. Kaliska, 21. Dobrogoszcz.

The following developmental stages of *Luronium natans* stems have been distinguished:
(1) seedling – stem with cotyledons and a small primary root, (2) juvenile – several leaves, initial outline of root system, (3) mature – fully-developed leaf rosette and well-developed root system, (4) generative – a flowering and fruiting stem.

To determine the environmental conditions prevailing in *Luronium natans* population areas, six sediment samples 0.25 dm^3 from each lake were collected and just as many near-sediment water samples (0.5 dm^3). Sediment samples, from the root system of *Luronium natans*, were used for determining the pH, TP and Ca concentration and organic matter content. In the near-sediment water samples the following: DOC, colour, TP were determined additionally according to the methods suggested by Golterman (1975), Hermanowicz *et al.* (1999). The total phosphorus (TP) was determined by the molybdate method using ascorbic acid as a reductor (Greenberg *et al.* 1992), whereas DOC by the spectrophotometric method (Moore 1985, 1987, Collier 1987, Górniak 1995). The concentration of DOC was read out from the calibration curve obtained as a DOC dependence on absorbency (A_{330}).

3. RESULTS

3.1. Impact of environmental conditions on *Luronium natans* population density

In the lake series under study, the highest *L. natans* population density is found in lightly acid to weakly alkaline water bodies. In very acid lakes (pH<5.0) the density reaches the level of 437.5±116.4 stems m^{-2}, in lightly acid, neutral and weakly alkaline 857.5±389.7 stems m^{-2}, and in alkaline 190.0±233.1 stems m^{-2} ($P < 0.05$; Table 1).

Table 1. Characteristics of *Luronium natans* populations in lakes with different range of site parameters.

Site parameter	No. of lakes	Density [stems m^{-2}] X±s.d.	Generative stem frequency [%] X±s.d.	Seedling frequency [%] X±s.d.	Aggregation size [m^2] Me
pH			n=42	n=42	n=42
n=57					
<5.0	2	437.5±116.4	5.3±4.0	9.6±8.8	65.40
5.0–6.0	2	857.5±389.7	15.1±16.8	10.1±5.3	2.80
6.1–7.0	4	858.7±324.9	18.2±22.8	10.1±4.6	3.72
7.1–8.0	3	758.3±502.4	14.4±20.9	20.0±8.8	0.23
>8.0	3	190.0±233.1	56.1±44.0	1.7±2.7	0.04
DOC [mg C dm^{-3}]		n=51	n=51	n=51	n=66
<3.5	3	706.6±302.3	8.4±7.7	9.4±6.9	1.70
3.5–5.0	6	695.7±423.4	20.3±17.8	14.7±8.9	9.71
5.1–6.0	3	1070.0±377.1	4.0±3.4	11.3±4.3	3.13
>6.0	4	205.0 ±199.3	44.1±43.4	2.9±3.4	0.51
TP [μg dm^{-3}]		n=45	n=45	n=45	n=67
<10.0	1	395.0±111.8	17.0±18.9	12.9±8.5	0.94
10.0–15.0	4	815.2±277.7	11.8±13.2	11.8±7.7	22.90
15.1–20.0	4	770.0±405.0	2.3±3.6	10.2±5.4	2.14
20.1–30.0	3	951.6±405.6	26.2±24.1	14.7±10.4	0.06
>30.0	3	80.0±61.6	77.1±38.3	0	0.02
$C_{org.}$ in the sediment [% C]		n=51	n=51	n=51	n=99
<5.0	5	281.0±223.5	50.7±35.0	7.5±7.9	0.24
5.1–10.0	5	941.0±446.8	9.9±10.4	15.8±10.5	0.34
10.1–30.0	4	526.2±232.2	2.0±3.7	11.7±8.1	3.24
>30.0	3	560.0±314.8	14.8±20.33	10.1±7.4	19.90
Depth [m]		n=57	n=57	n=57	n=81
<0.2	5	87.0±44.5	98.0±9.0	0	0.43
0.2–1.0	5	271.0±153.0	41.6±36.4	8.5±7.4	0.52
1.1–2.0	4	695.0±389.8	4.4±3.8	12.6±8.4	1.77
>2.0	5	914.0±329.1	10.5±12.0	10.0±5.0	11.21

Under DOC conditions ranging from 3.5 mg C dm^{-3} to 6.0 mg C dm^{-3} the highest population density is found in sites where the content of DOC varies between 5.0 mg C dm^{-3} and 6.0 mg C dm^{-3} (Fig. 2, Table 1). Concentrations above 6.0 mg C dm^{-3} are too high for this plant; it is manifested by a considerable thinning of its populations (205.0±199.3 stems m^{-2}, $P < 0.05$). Along the phosphorus concentration gradient from <10.0 μg TP dm^{-3} to >30.0 μg TP dm^{-3}, the highest population density (951.6±405.6 stems m^{-2}) was recorded for the 20.0 μg TP dm^{-3} - 30.0 μg TP dm^{-3} interval (Fig. 3, Table 1). At phosphorus concentrations above 30.0 μg TP dm^{-3} a rapid decrease in population density occurred, to as low as 80.0±61.6 stems m^{-2} ($P < 0.05$). On inorganic substrates (<5.0% C) *Luronium natans* population density is usually lower than on mineral-organic substrates (Table 1). Tests for the content of organic carbon in the substrates indicate that the plant under study prefers inorganic sediments mixed with small amounts of organic matter (5.0–10.0% C). An increase in depth from 0.2 to >2.0 m is followed by a population density increase (Fig. 4), which most likely is the result of the increasingly high organic matter content in the sediment. The low population density found in shallow sites to the depth of 0.2 m is the result of a considerable wave-caused damage.

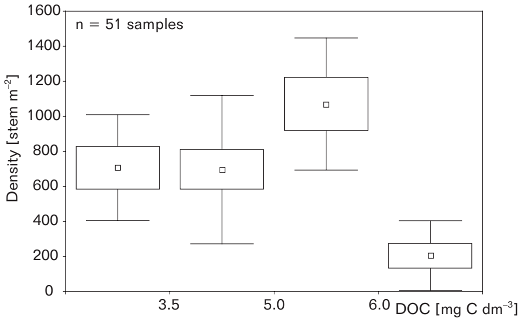

Fig. 2. Density of stems of *Luronium natans* in sites varying in dissolved organic carbon (DOC) concentration in the water (mean value, standard error; No. of lakes see Table 1).

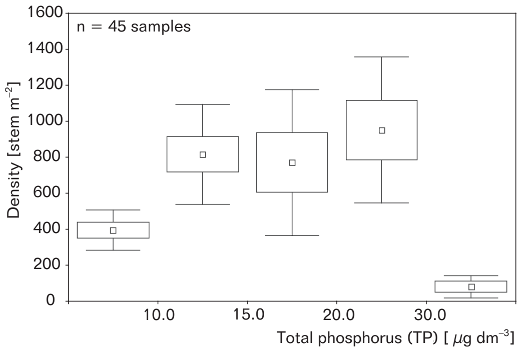

Fig. 3. *Luronium natans* population density in sites differing in phosphorus concentration in the water (mean value, standard error; No. of lakes see Table 1).

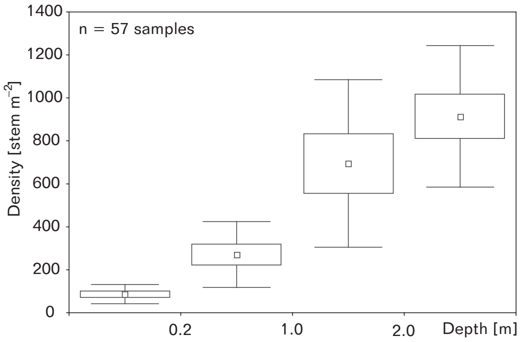

Fig. 4. *Luronium natans* population density in depth intervals (mean value, standard error; No. of lakes see Table 1).

3.2. Proportion of generative stems in *Luronium natans* populations

In habitats with pH levels varying between <5.0 and 8.0 the numerical proportion of generative stems attains the range of 5.3–56.1% ($P < 0.05$), being the lowest (5.3%) in very acid lakes, which may indicate a decrease in generative reproduction (Fig. 5, Table 1). A low DOC concentration does not limit the size of the generative stem fraction in a population, but a high one seems to favour its increase (Table 1). However, it must be stressed that the correlation between the number of flowering and fruiting stems and DOC concentration is rather weak. An increase in phosphorus concentration does not significantly affect the number of flowering and fruiting stems. The proportion of generative stems in a population slightly depends on phosphorus concentration in the water, although at a higher concentration a larger number of stems flower and fruit was found (Table 1). The largest proportion of *L. natans* stems (50.7±35.0%) flower and fruit on inorganic substrates, poor in organic carbon. On this kind of substrate most of the stems that become mature in a given year produce flowers and fruits. It follows from this that a substrate which is poor in organic carbon provides optimum conditions for the reproduction of this plant (Table 1; Fig. 6). An increase in organic matter content impedes the generative reproduction. Depth affects also the size of the generative stem fraction in a population. Close to the shore (<0.2 m) nearly all stems (98±0.9%) are generative, whereas in substrate zones below 2 m their proportion is as low as 10.5% (P <0.05).

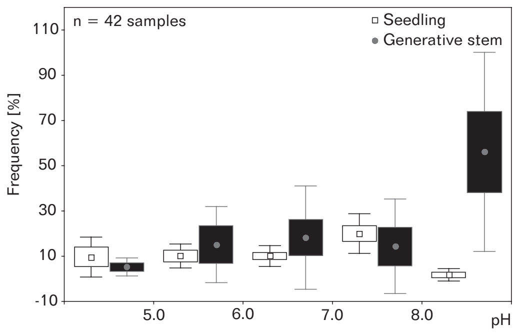

Fig. 5. Frequency (%) of *L. natans* generative stems and seedlings in sites varying in pH (mean value, standard error; No. of lakes see Table 1).

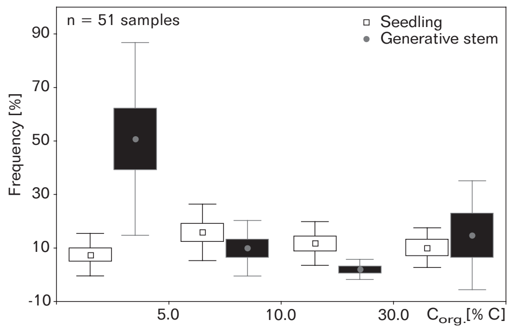

Fig. 6. Frequency (%) of *L. natans* generative stems and seedlings under a variable organic matter content in the sediment (mean value, standard error; No. of lakes see Table 1).

3.3. Seedling proportion in a population

There are very few seedlings in *L. natans* populations. In waters with pH between 5 and 7 the arithmetic mean of the proportion of seedlings equals 10.1±4.6%, in neutral and weekly alkaline 20±8.8% (P <0.05), while in clearly alkaline waters seedlings occur sporadically (Fig. 5). It follows from this that pH levels above 8.0 may impede seed germination. Genets represent small proportions in *Luronium natans* populations (Table 1). At DOC concentrations ranging from <3.5 to 6.0 mg C dm^{-3} the frequency of seedlings in a population stays at the level of about a dozen percent (Table 1). In waters with a very low (<3.5 mg C dm^{-3}) and very high (>6.0 mg C dm^{-3}) DOC content a lower seedling frequency is found, not exceeding 10%. Phosphorus concentration in the water probably has no effect on the number of seedlings in a population (Table 1). It may follow from this that phosphorus does not impede seed germination or affect seedlings survival, although at concentrations above 30.0 μg TP dm^{-3} no seedlings were found. On mineral (inorganic) substrates (<5.0% C) few 7.5±7.9% *Luronium natans* seedlings occurred, but their percentage was much higher on mineral-organic (5.0–10.0% C) substrates (Fig. 6). The higher seedling proportion most probably resulted from a higher population density in those sites. It is worthwhile to note that the abundance of seedlings in populations increases with increasing depth, being the highest at the depth range of 1.1–2.0 m (Table 1).

3.4. Aggregation size

The size of *Luronium natans* aggregations depends on the lake water pH. In very acid (pH<5.0) lakes they attain the largest area (Me = 65.4 m^2), in weakly acid to neutral waters they are small (3.7 m^2), and in alkaline (pH>8.0) – very small (0.04 m^2). This indicates that aggregation size, though highly variable, is negatively correlated with the water pH. A similar relationship is found in regard for DOC concentrations in the water. The threshold concentration level is 6.0 mg C dm^{-3} at which *L. natans* aggregations attain the smallest area, about 0.5 m^2 (Table 1). In regard for the concentration of phosphorus, aggregations of the largest area can be found in lakes with a low concentration of this element (10.0–15.0 μg TP dm^{-3}). It means that in lakes which are very poor in nutrients and in nutrient-rich ones (>30.0 μg TP dm^{-3}) this plant, as a rule, fails to form large aggregations (Table 1). The smallest (0.24 m^2) aggregations are found on inorganic (<5.0% C), and the largest

(19.9 m^2) on organic sediments. It should be mentioned here that the aggregation area strongly depends on the depth at which the aggregations occur, and there exists a direct relationship: the greater the depth, the larger the *L. natans* aggregations. Aggregations of the largest size occur close to the lower depth range of the population area.

4. DISCUSSION

Communities of submerged plants are most often characterized by the dominance of one or several species. According to Szmeja and Bociąg (in press), the susceptibility of the dominant species to habitat conditions is fundamental of importance for the dynamics of aquatic vegetation. *Luronium natans* is not a dominant species, and does not form its own communities either (Matuszkiewicz 2001). For this reason, it can be classified as a rather weak competitor (Greulich 1999).

L. natans occupies habitats 0.1 to 3.0 m deep, mainly in slightly acid, nutrient-poor and clear waters. Under such conditions it forms the best-formed and most fecund stems (Bazydło and Szmeja 2004). This plant reproduces mainly vegetatively, and its seedlings represent a low proportion as, 9.5%, of the population. Average population density amounts to 591.0 stems m^{-2}. The percentage of genets is similar to that in other aquatic plant populations (Szmeja 1987c).

The greater the depth, the larger and denser the *Luronium natans* aggregations (Table 1). However, the proportion of seedlings in the aggregations is small. This situation confirms Łomnicki`s view (1980) that at high population densities the plants increase their chance to survive by investing primarily in the maintenance of their current social status in a population, and limiting expenditure on reproduction. A similar relationship was observed also in *Lobelia dortmanna* populations (Szmeja 1987a), where mainly vegets occurred in the populations on greater depth. The cause of the low proportion of genets probably is related to the variation of the characteristics of the aquatic environment. With increasing depth the temperature drops, due to which plant growth is retarded, the possibility to attain the reproductive phase in a given year becomes less probable, and at the same time seed germination is impeded. A deterioration of light conditions may cause similar changes (Szmeja 1987b, c).

Optimum conditions for *L. natans* growth exist in slightly acid lakes (Table 1, Fig. 5) where this plant forms fairly large and very dense aggregations. According to Bazydło and Szmeja (2004), in such lakes the best-formed and most fecund *Luronium natans* individuals are found. Very acid ($pH<5$) or very alkaline ($pH>8.0$) waters are unsuitable for this plant. Low pH levels of lakes result from their acidification or enrichment with humic substances (HS) which considerably reduce macrophyte populations (Szmeja and Bociąg in press). In humic lakes, HS bring about far-reaching changes in light conditions, mainly due to the presence of a large amount of colloidal suspensions in the water (Gjessing 1976, Górniak 1996, Wilkinson *et al.* 1997), which increase the absorption of light over the 200–365 nm range (Frimmel 1994). As indicated by the present studies, *Luronium natans* tolerates HS concentrations up to the level of 6 mg C dm^{-3}. Below this level its aggregations are larger and denser, and its individuals are better-formed and produce more offspring (Bazydło and Szmeja 2004). Low HS concentrations appear to be suitable for *L. natans*, while high ones (>10 mg C dm^{-3}) cause extinction of this species, as well as of other cormophytes, and of bryophytes and some charophytes (Szmeja 2000, Szmeja *et al.* 2001).

Another important factor determining the population structure of *Luronium* is the concentration of phosphorus in the lake water. Concentrations of this element ranging from 10.0 to 30.0 μg TP dm^{-3} are favourable for this plant. Above the level 30.0 μg TP dm^{-3} phosphorus causes the retreat of *L. natans* from lakes. This process is manifested by a reduction in aggregation size already at concentrations above 20.0 μg TP dm^{-3}, which indicates the beginning of aggregation disintegration and elimination of *Luronium natans*. Harmful to macrophytes are above all the effects of lake eutrophication. The most important of them is the increase in abundance and biomass of the periphyton which reduces light and affects the amount and availability of resources, including carbon for photosynthesis (Carpenter *et al.* 1998).

Sediment, depending on its composition, regulates the size of populations. On inorganic substrates *L. natans* forms small aggregations of which nearly all individuals (98%) flower and fruit in summer. Data from studies of *Lobelia dortmanna* indicate quite a different situation: in inorganic, nutrient-poor habitats population density was higher than in organic, comparatively rich, habitats (Szmeja 1987a). In the case of *Luronium natans*, an increase in the content of organic carbon in the substrate (5.0–10.0% C) is followed by an increase in population size and density, and decrease of the proportion of generative individuals.

Excessive concentrations of carbon and phosphorus, and alkaline water pH impede the population growth. Aggregations are small and few in number, but the proportion of generative individuals in them is high (up to 98%). The rule "something for something" becomes evident: vegetative propagation is to a large extent replaced by generative reproduction (Huston and Smith 1987). Inhibition of vegetative propagation may, particularly in clonal plants, limit the production of new individuals (Harper 1977, Cook 1985).

It has been reported that large aggregations favour the survival of individuals, but excessively large and dense aggregations may deplete the nutrient resources in habitats and take up all free space (Andrzejewski and Falińska 1986).

Aggregation size depends on the depth at which the plants grow. Other environmental factors such as the water pH and content of nutrients to a minor extent affect the aggregation size, but these characteristics vary considerably in the lake littoral. It should be mentioned also that the competitive power of *Luronium natans* is low (Greulich and Bornette 1999), from which it may follow that the significant factor limiting the expansion of this plant is probably the availability of unoccupied spaces. Paradoxically, *Luronium* finds optimum conditions for aggregation formation at the depth range of 1–2 m, but it is where the majority of aquatic plants grow, e.g. *Lobelia dortmanna*, *Littorella uniflora*, *Isoëtes lacustris* and *Myriophyllum* (Rich and Jermy 1998, Szmeja 2001).

5. SUMMARY

The structure of *Luronium natans* (L.) Raf. populations (distribution of aggregation, density and age-structure of population) were studied in 21 lakes in the Pomeranian Lakeland (NW Poland, Fig. 1), where the highest population density is found in slightly acid pH (6–7) waters, poor in DOC (<6.0 mg C dm^{-3}) and phosphorus (<30.0 μg TP dm^{-3}; Table 1, Figs. 2, 3). *Luronium natans* propagates mainly vegetatively and prefers shallow (1–2 m), mineral-organic substrates (5.1–10.0% C; Table 1, Fig. 6). Seedlings represent about 10% of a population. High pH levels (pH>8.0), concentration of carbon (>6.0 mg C dm^{-3}) and phosphorus (>30.0 μg TP dm^{-3}) in the water impede the population growth. Under such conditions population density is smaller even by 80–90%, aggregations are smaller, but the proportion of generative stems is higher. Aggregation area depends on the depth: the deeper the location – the larger and denser the aggregations, the shallower the location – the higher the percentage of generative individuals (up to 98% of the population composition).

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6. REFERENCES

Alpert M., Mooney H. A. 1986 – Resource sharing among ramets in the clonal herb *Fragaria chiloensis* – Oecologia, 70, 227–233.

Alpert P. 1991 – Nitrogen sharing among ramets increases clonal growth in *Fragaria chiloensis* – Ecology, 72: 69–80.

Andrzejewski R., Falińska K. 1986 – Populacje roślin i zwierząt [Plant and animal populations] – Wyd. Nauk. PWN, Warszawa, 442 pp. (in Polish)

Barrat-Segretain M. H., Amoros C. 1996 – Recolonization of cleared riverine macrophyte patches: importance of the border effect – J. Veg. Sci. 7: 769–776.

Barrat-Segretain M. H., Bornette G., Hering-Vilas-Bôas A. 1998 – Comparative abilities of vegetative regeneration among aquatic plants growing in disturbed habitats – Aquat. Bot. 60: 201–211.

Bazydło E., Szmeja J. 2004 – The effect of pH, dissolved organic carbon and total phosphorus concentration on selected life history traits of *Luronium natans* L. (Raf.) – Pol. J. Ecol. 52: 191–200.

Carpenter S. R., Cole J. J., Kitchell J. F., Pace M. L. 1998 – Impact of dissolved organic carbon, phosphorus, and grazing on phytoplankton biomass and production in experimental lakes. – Limnol. Oceanogr. 43: 73–80.

Casper S. J., Krausch H. D. 1980 – Süßwasserflora von Mitteleuropa. Pteridophyta und Anthophyta, Band 23 – Gustav Fischer Verlag, Stuttgart.

Collier K. J. 1987 – Spectral properties of some West Coast waters and their relationship with dissolved organic carbon – Mauri Ora 14.

Cook R. E. 1985 – Growth and development in clonal plant populations (In: Population biology and evolution in clonal organisms, Eds.: J. B. L. Jackson, L. W. Buss, R. F. Cook) – Yale Uniiv. Press, New Haven. pp. 259–296.

Coops H., van den Brink F. W. B., van der Velde G. 1996 – Growth and morphological responses of four helophytes species in an experimental water-depth gradient – Aquat. Bot. 54: 11–24.

Falińska K. 2002 – Przewodnik do badań biologii i ekologii populacji roślin [A guide to researches into the biology and ecology of plant populations] (In: Vademecum Geobotanicum 4, Ed. J. B. Faliński) – PWN, Warszawa, 586 pp. (in Polish)

Fischcer M., Matthies D. 1998 – The effect of population size on performance in the rare plant *Gentianella germanica* – Journal of Ecology, 86: 195–204.

Frimmel F. W. 1994 – Photochemical aspects related to humic substances – Environ. Int. 20: 373–386.

Gjessing E. T. 1976 – Physical and chemical characteristic of aquatic humus – Ann. Arbor. Science Publ. Inc., Ann Arbor.

Golterman H. J. 1975 – Physiological Limnology – Elsevier, Amsterdam, 489 pp.

Górniak A. 1995 – Spektrofotometryczna metoda oznaczania stężeń i jakości rozpuszczonego węgla organicznego w wodach [A Spectrophotometric method for determining the concentrations and quality of dissolved organic carbon in waters] – Gosp. Wodna 2: 31–33. (in Polish)

Górniak A. 1996 – Substancje humusowe i ich rola w funkcjonowaniu ekosystemów słodkowodnych [Humic substances and their role in the functioning of freshwater ecosystems] – Dział Wydawnictw Filii Uniw. Warszawskiego, Białystok. (in Polish)

Greenberg A. E., Clesceri L. S., Eaton A. D. 1992 – Standard methods for the examination of the water and wastewater – American Public Health Association, 18th edition, Washington.

Greulich S. 1999 – Competition, parturbations et produticite potentielle dans la definition de l'habitat d'especes rares: Etudes experimentale du macrophyte aquatique *Luronium natans* (L.) Rafin. – Univ. Claude Bernard, Lyon 1, France.

Greulich S., Bornette G. 1999 – Competitive abilities and related strategies in four aquatic species from an intermeditely disturbed habitat – Freshwat. Biol. 41: 493–506.

Greulich S., Bornette G., Amoros C., Roelofs J. G. M. 2000 – Investigation on the fundamental niche of a rare species: an experiment on establishment of *Luronium natans* – Aquat. Bot. 66: 209–224.

Harper J. L. 1977 – Population Biology of Plants – Acad. Press, London.

Hermanowicz W., Dożańska W., Dojlido J., Koziorowski B. 1999 – Fizyczno-chemiczne badanie wody i ścieków [Physico-chemical studies of water and sewage] – Arkady, Warszawa, 847 pp. (in Polish)

Huston M., Smith T. 1987 – Plant succession: life history and competition – Am. Nat. 130, 2: 168–198.

Jonsdottir I. S., Callaghan T. V., 1990 – Intraclonal translocation of ammonium and nitrate in *Carex bigelowii* using ^{15}N and nitrate reductase assays – New Phytol. 114: 419–428.

Jonsdottir I. S., Watson M. A. 1997 – Extensive physiological integration (In: The ecology and evolution of clonal plants, Eds.: H. De Kroon, J. van Groenendael) – Backhuys Publishers, Leiden.

Kéry M., Matthies D., Spillmann H. H. 2000 – Reduced fecundity and offspring performance in small populations of the declining grassland plants *Primula veris* and *Gentiana lutea* – Journal of Ecology, 88: 17–30.

Łomnicki A. 1980 – Zróżnicowanie osobników a regulacja zagęszczenia populacji [Diversity of individuals and population density regulation] – Wiadomości ekologiczne 26, 4: 361–390. (in Polish)

Matuszkiewicz W. 2001 – Przewodnik do oznaczania zbiorowisk roślinnych Polski [A guide to the plant communities of Poland] (In: Vademecum geobotanicum, Ed. J. B. Faliński) – PWN, Warszawa, 586 pp. (in Polish)

Moore T. R. 1985 – The spectrophotometric determination of dissolved organic carbon in peat waters – Soil Sci. Soc. Ann. J. 49: 1590–1592.

Moore T. R. 1987 – An assessment of a simple spectrophotometric method for the determination of dissolved organic carbon in freshwaters – New Zeal. J. Mar. Fresh. Res. 21: 585–589.

Price E. A. C., Marshall Ch. 1999 – Clonal plants and environmental heterogeneity – Plant Ecology 141: 3–7.

Rich T. C. G., Jermy A. C. 1998 – Plant Crib 1998 – Botanical Society of British Isles, London.

Steufer J. F., de Kroon H., During H. J. 1996 – Exploitation of environmental heterogeneity by spatial division of labour in a clonal plant – Funct. Ecol. 10: 228–334.

Stuefer J. F., During H., de Kroon H. 1994 – High benefits of clonal integration in stoloniferous species in response to heterogeneous light environments – Journal of Ecology, 82: 511–518.

Symonides E. 1979 – The structure and population dynamics of psammophytes in inland dunes. Population phenomena as a phytocenose-forming factor (a summing-up discussion) – Ekol. pol. 27, 2: 259–281.

Szmeja J. 1987a – The structure of a population of *Lobelia dortmanna* L. along a gradient of increasing depth in an oligotrophic lake – Aquat. Bot. 28: 1–13.

Szmeja J. 1987b – The ecology of *Lobelia dortmanna* L. III. The plasticity of individuals along a gradient of increasing depth in oligotrophic lakes – Ekol. pol. 3: 545–558.

Szmeja J. 1987c – The ecology of *Lobelia dortmanna* L. II. Population structure and dynamics within a constant depth interval in oligotrophic lakes – Ekol. pol. 35: 523–544.

Szmeja J. 1992 – Struktura, organizacja przestrzenna i demografia populacji isoetydów Studium ekologiczne roślin podwodnych [Structure, Spatial Organization and Demography of Isoetid Populations. Ecological Studies of Submerged Aquatic Plants] – Uniwersytet Gdański. Rozprawy i Monografie, 175: 1–137. (in Polish)

Szmeja J. 1994 – An individual's status in populations of isoetid species – Aquat. Bot. 48: 203–224.

Szmeja J. 2000 – Tendencies of changes in the flora and vegetation structure of Pomeranian lakes under the influence of humic substances (In: Mechanisms of anthropogenic changes of the plant cover, Eds.: B. Jackowiak, W. Żukowski) – Bogucki Wyd. Naukowe, Poznań, pp. 85–98.

Szmeja J. 2001 – *Luronium natans* L. (Rafin.) (In: Polska Czerwona Księga roślin [Polish Red Data Book of Plants], Eds.: K. Zarzycki, R. Kaźmierczakowa) – PAN, Kraków, pp. 395–396. (in Polish)

Szmeja J., Bazydło E., Uruska A. 2001 – Role of humic substances in the determination of *Sphagnum denticulatum* Brid. and *Myriophyllum spicatum* L. habitat conditions – Pol. J. Ecol. 49, 2: 101–113.

Szmeja J., Bociąg K. in press – The deterioration of populations of underwater plants in soft water lakes enriched with acidic organic matter – Acta. Soc. Bot. Pol.

Van Groenendael J., Klimes J. M., Klimesova J., Hendriks R. J. 1996 – Comparative ecology of clonal plant – Phil. Trans. Roy. Soc. Lond. B. 351: 1331–1339.

Van Groenendael J. M., de Kroon H. 1990 – Clonal growth to plants: regulation and function – SPB Acad. Publ., The Hudge.

Wilkinson K. J., Negre J. C., Buffle J. 1997 – Coagulation of colloidal material in surface waters: the role of natural organic matter – Journal of Contaminant Hydrology 26: 22–243.

Willby N. J., Eaton J. W. 1993 – The distribution, ecology and conservation of *Luronium natans* L. Rafin. In Britain – J. Aquat. Plant Manage. 31: 70–76.

Zarzycki K. 1965 – Obecny status badań nad konkurencją /współzawodnictwem/ roślin wyższych. [Current status of research into higher-plant competition] – Ekol. pol. B 11(3): 195–210. (in Polish)

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