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## EFFECT OF PH, DISSOLVED ORGANIC CARBON AND TOTAL PHOSPHORUS CONCENTRATIONS ON SELECTED LIFE HISTORY TRAITS OF *LURONIUM NATANS* (L.) RAF.

**ABSTRACT:** A hypothesis has been put forward that low pH or high concentration of total phosphorus (TP) and dissolved organic carbon (DOC) in the lake water are the factors responsible for observed extinction of the population of *Luronium natans* (L.) Raf., protected macrophyte species from the group of isoetids. A study was performed on 525 generative individuals collected from 21 lakes in Pomeranian Lakeland (NW Poland) and a correlation between the biometric characteristics and environmental conditions in the lakes was tested. The following life history traits have been analysed: size of individuals, their fecundity and allocation of biomass. The greatest and most fecund individuals grow in the lake water of pH 6.1–7.0, poor in TP (10.1–20.0  $\mu\text{g dm}^{-3}$ ) and DOC (3.5–6.0  $\text{mg C dm}^{-3}$ ). The allocation of biomass of the individuals growing in the optimum conditions is as follows 46–54% in the leaves, 22–31% in the roots and 20–27% in the rhizome. In the lakes with water of pH < 5.0 or of TP > 20.1  $\mu\text{g dm}^{-3}$  and DOC > 6  $\text{mg C dm}^{-3}$ , a statistically significant decrease in the size of the individuals and unfavourable changes in the biomass allocation are found. The main environmental factor responsible for dying out of local populations of *Luronium natans* is a decrease of pH below < 5.0.

**KEY WORDS:** life history traits, macrophyte, *Luronium natans*, dissolved organic carbon, total phosphorus, plant protection

### 1. INTRODUCTION

*Luronium natans* is aquatic evergreen perennial rooted in substrate which occurs in north-western and central Europe (Hultén and Fries 1986). It is a stoloniferous and rosette forming plant, of vegetative and generative modes of reproduction, flowering and fructifying from May to September (Szmeja 2001). The species grows in soft-water lakes poor in calcium (Szańkowski and Kłosowski 2001), with sand, mud or peat bottom deposits (Dąbbska 1965, Arts and Den Hartog 1990, Smits *et al.* 1990, Weeda *et al.* 1991).

In north-western and central Europe *Luronium natans* is a species threatened with extinction and has been included on the list of special protection plants prepared for EU countries, (in 'Nature 2000' position 1831). In Poland it also belongs to the group of species threatened with extinction. Till the middle of the 20<sup>th</sup> cen-

tury this plant occurred in 120 lakes of western Poland, whereas at present it grows only in 63 lakes. The rate of extinction of this species is very high and can be approximated as one lake per year. The reasons for its extinction are linked with human impact (Szmeja 2001).

The aim of the study is to indicate the environmental factors responsible for dying out of local populations of this species. On the basis of a preliminary study a hypothesis is put forward that the extinction of this species is related to a too low pH of the lake water or a too high concentration of total phosphorus (TP) and dissolved organic carbon (DOC) in lake water. The unfavourable changes in these environmental factors are anthropogenic eutrophication, acidification or humification of lakes (anthropogenic inflow of allochthonous humic substances). It is assumed that the extinction of this species is preceded by changes in allocation of biomass, as well as a decrease in the size and fecundity of individuals in a given population. Possible reasons for the extinction of local populations are changes in the plants morphology induced by the environment.

## 2. METHODS

The study was performed in the vegetation season July of 2001 and 2002, in 21 lakes of the Pomeranian Lake District (NW Poland; Fig. 1). From each lake 25 randomly selected flowering or fructifying individuals were collected (the total number of individuals = 525), at the depth of 0.5–1.0 m, from the sandy-gravel lake sediment with a small contribution of detritus and from the plant aggregations of similar population density. The same-age individuals were subjected to biometric analysis taking into account the following life history traits: biomass allocation, size and fecundity. The parameters measured included: (1) the length and width of each leaf ( $n = 6140$ ); (2) total length of roots in the root system ( $n = 525$ ) by the Tennant method (1975); (3) number of flowers and fruits on each plant ( $n = 525$ ). On the basis of the measurements the following characteristics of plants were calculated: the assimilation area of each individual [ $\text{cm}^2$ ], fecundity of each individual expressed as a sum of the number of flowers and fruits

and the length of roots in the root system [cm]. After biometric measurements, the plants were dried at  $80^\circ\text{C}$  to constant weight and weighted to an accuracy of  $\pm 0.001$  g, in order to estimate biomass allocation in particular organs of the plant (leaves, rhizome, roots). The data were processed by statistical analyses usually applied in biometry (Sokal and Rohlf 1995). An additionally calculated parameter was Coefficient of Variance (CV), being a product of a standard deviation in a sample studied ( $n$ ) and the arithmetic mean of a given parameter.

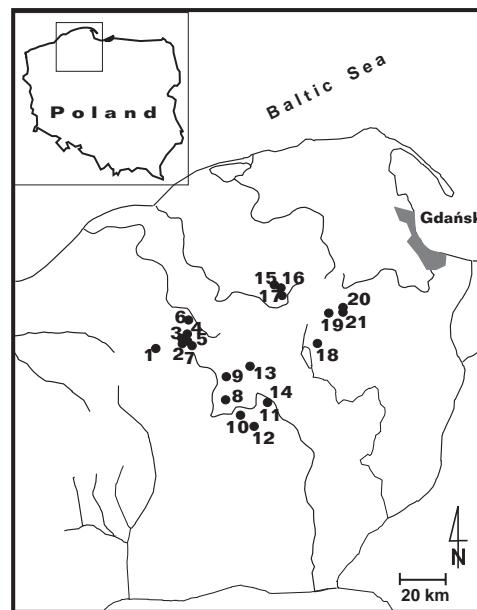


Fig. 1. Location of the lakes under study (1–21) in NW Poland (Pomeranian Lakeland).

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.

At the sites occupied by *L. natans* populations the bottom sediment and water from the above-sediment layer were subjected to chemical analysis. From each lake 6 samples of bottom sediment of  $0.25 \text{ dm}^3$  and 6 samples of water from the near-sediment layer of  $0.5 \text{ dm}^3$  were taken. The sediment samples were taken from the root system of plants. In the sediment samples the pH value, concentrations of total phosphorus (TP),  $\text{Ca}^{2+}$  and organic matter were estimated, while water samples were additionally

characterised by DOC and colour, according to the method given 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, Górnaiak 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. The environmental conditions in the sites of *Luronium natans*

*Luronium natans* grows in lake water of pH 4.5–8.8, poor in calcium ions (1.3–18.4 mg Ca dm<sup>-3</sup>) and nutrient deficient (Table 1). The concentration of TP in water from the near-sediment layer varies in the range 7.8–56.4 mg dm<sup>-3</sup>, water is transparent (1–40 mg Pt dm<sup>-3</sup>), which is a consequence of a low concentration of DOC (2.7–11.1 mg C dm<sup>-3</sup>; Me = 4.3).

The sediment from the population sites is mineral (Me = 7.8% C g<sup>-1</sup> d.w.),

poor in calcium (0.9–3.2 mg Ca g<sup>-1</sup> d.w.; Me = 1.8) and usually acid (pH 4.2–7.4; Me = 5.6). *Luronium natans* grows at the depths of 0.1–3.4 m (Me = 1.2), in bottom deposits poor in TP (14.8–174 µg TP g<sup>-1</sup> d.w.; Me = 37.2), usually in sites of weak wind waves (Table 2).

#### 3.2. The effect of pH

**In highly acid water (pH < 5.0)** generative individuals of *L. natans* are the smallest (Fig. 2, Table 3). The reason is first of all a significant decrease in the assimilative area and the root system. The biomass allocation in the above-ground (leaves and rhizome) and underground parts (roots) varied significantly (0.8–4.6 g d.w.; Me = 2.1), mainly as a result of disproportionate relations between the leaf and root biomass. The leaves make about 46%, roots – 34% and the rhizome – 20% of biomass of an individual (Table 4). The ranges of variation of each of these mass allocations are small. The ratio of the biomass of the above-ground organs (leaves and rhizome) to that of the underground organs (roots) is  $2.2 \pm 1.0$ . This means that over half of the mass (66%) is allocated in the leaves and

Table 1. Near-bottom water characteristic in 21 lakes with *Luronium natans* in North-Western Poland (July 2001, 2002). Lakes were listed along the increase of pH; location of lakes (No.) – see Fig. 1.

LAKE	pH	Colour [mg Pt dm <sup>-3</sup> ]	DOC [mg C dm <sup>-3</sup> ]	Ca [mg dm <sup>-3</sup> ]	TP [µg dm <sup>-3</sup> ]
Sporacz (11)	4.5–4.8	13	3.7±0.1	1.7±0.1	19.4±0.3
Krasne (9)	4.7–5.0	3	2.8±0.1	2.5±0.1	11.3±0.5
Moczadło (14)	5.3–5.5	1	3.3±0.2	3.3±0.1	7.8±0.5
Smółowe (4)	5.3–5.6	5	3.6±0.2	3.0±0.1	11.6±0.4
Linowskie (10)	5.6–5.7	14	3.4±0.2	2.0±0.1	17.1±0.5
Nowoparszecenickie (13)	5.6–5.7	23	3.6±0.1	1.3±0.1	13.2±1.3
Piasek (7)	6.0–6.6	3	2.9±0.1	4.1±0.1	12.0±0.2
Okoń (12)	6.2–6.3	28	4.6±0.2	4.4±0.1	19.0±1.1
Bobięcińskie (1)	6.2–6.7	38	4.9±0.3	4.8±0.2	17.5±0.5
Orle (2)	6.3–6.4	26	5.3±0.2	4.3±0.1	13.2±0.8
Kaliska (20)	6.6–6.7	55	6.8±0.3	2.0±0.1	27.6±0.1
Kamień (3)	6.6–6.7	17	5.9±0.1	6.8±0.2	12.4±0.6
Ostrowite (15)	6.7–6.8	66	10.6±0.3	3.9±0.1	31.1±1.3
Święte (6)	7.0–7.1	13	3.7±0.3	7.2±0.1	29.1±1.0
Dobrogoszcz (21)	7.0–7.5	18	4.3±0.1	7.7±0.3	28.8±1.4
Dolskie (5)	7.3–7.5	16	4.3±0.1	14.5±0.1	18.3±0.7
Świniebudy (19)	7.6–7.7	20	3.6±0.2	4.5±0.3	37.7±1.1
Baroczno (17)	7.8–8.4	40	6.8±0.2	3.9±0.1	56.4±1.9
Drzędno (18)	7.9–8.1	34	6.8±0.2	4.3±0.2	31.9±0.2
Liny (8)	8.0–8.2	50	11.1±0.4	18.4±0.1	34.6±1.6
Warleńskie (16)	8.0–8.5	33	6.2±0.1	4.7±0.3	28.4±0.9

Table 2. Characteristics of sediments in 21 lakes with *Luronium natans* in North-Western Poland (July 2001, 2002). Lakes are listed according to pH; location of lakes (No.) – see Fig. 1.

LAKE	pH	C [% g <sup>-1</sup> d.w.]	Ca [mg g <sup>-1</sup> d.w.]	TP [μg g <sup>-1</sup> d.w.]
Smołowe (4)	4.2–4.4	22.6±2.2	1.9±0.1	74.0±16.0
Krasne (9)	4.5–4.6	64.1±0.6	1.6±0.1	63.2±0.3
Sporacz (11)	4.6–4.7	45.8±0.9	2.5±0.1	43.4±4.2
Moczadło (14)	4.8–4.9	0.9±0.3	1.1±0.5	13.6±0.7
Bobięcińskie (1)	4.9–5.2	7.1±1.7	1.2±0.2	103.5±1.3
Linowskie (10)	4.9–5.5	9.3±3.0	1.7±0.2	32.3±1.1
Nowoparszczenickie (13)	5.0–5.6	42.9±4.8	2.6±0.1	60.5±2.3
Kamień (3)	5.2–5.7	24.6±0.7	1.7±0.1	60.4±6.1
Orle (2)	5.4–5.5	28.6±11.1	3.2±0.1	52.9±0.8
Okoń (12)	5.4–5.6	3.4±0.3	2.2±0.1	17.3±0.3
Kaliska (20)	5.5–5.7	22.9±4.2	2.0±0.1	62.0±2.8
Piasek (7)	5.6–6.0	10.0±4.6	1.9±0.2	56.3±8.1
Święte (6)	5.9–6.0	26.6±0.9	1.1±0.1	17.7±0.3
Świniebudy (19)	6.0–6.4	5.6±3.6	1.4±0.2	28.7±4.4
Baroczno (17)	6.1–6.2	2.1±0.8	1.2±0.1	14.8±0.3
Dobrogoszcz (21)	6.1–6.2	4.4±0.5	0.9±0.1	45.9±4.4
Drzędno (18)	6.1–6.2	0.9±0.1	2.3±0.3	25.5±1.5
Dolskie (5)	6.1–6.3	3.4±1.0	1.3±0.2	21.7±0.3
Liny (8)	6.1–6.3	0.9±0.6	1.5±0.1	16.7±0.6
Warleńskie (16)	6.2–6.3	7.8±5.7	1.9±0.1	27.6±2.2
Ostrowite (15)	6.4–7.4	2.1±0.2	0.9±0.1	20.7±0.9

the rhizome. The assimilative area is small ( $17.4 \pm 6.7 \text{ cm}^2$ ,  $Me = 16.3$ ) and the roots are short ( $91.7 \pm 45.1 \text{ cm}$ ). An interesting feature is a large range of variation of root length (0.2–2.0 m). An individual in the generative phase produces a low number of flowers and fruits ( $3.8 \pm 3.2$ ;  $Me = 3.0$ ). In highly acidic water the range of variation of this character is very high (1.0–13.0).

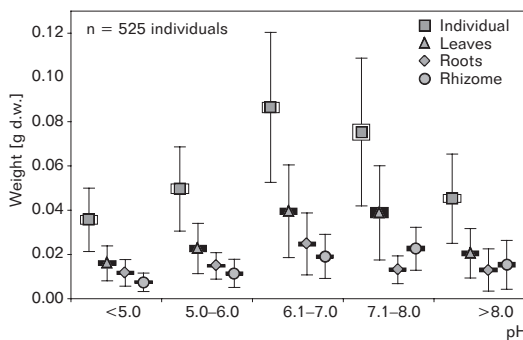


Fig. 2. Variation of the biomass of an individual plant, leaves, roots and rhizome in relationship to water pH (mean value, standard error, range; No. of lakes see Table 3).

**In water of pH 5.0–6.0** the leaves are greater (longer and wider), the rhizome is heavier and the roots are longer, so the weight of the plant increases ( $P < 0.05$ ; Fig. 2). The biomass allocation in the

leaves is 48%. In the two populations (the one at  $pH < 5.0$  and the one at  $pH 5.0–6.0$ ) the ratio of the biomass allocated in the aboveground and underground parts is similar (2.2 and 2.4, respectively). The biomass of the aboveground organs makes 70% of the total biomass of an individual (an increase = 6%;  $P < 0.05$ ), which follows first of all from a considerable increase in the assimilative area ( $26.0 \pm 12.4 \text{ cm}^2$  against  $17.4 \pm 6.7 \text{ cm}^2$ ;  $P < 0.05$ ). Changes in the root length are statistically insignificant. The most important response of the plant is an increase in the number of flowers and fruit ( $P < 0.001$ ), which means that in water of  $pH 5.0–6.0$  the individuals of *Luronium natans* are greater and more fecund than in water of  $pH < 5.0$ .

**In water of pH 6.1–7.0** the *Luronium natans* individuals are the greatest and most fecund (Fig. 2, Table 3). Relative to the individuals collected from water of  $pH 5.0–6.0$  the ones collected from water of  $pH 6.1–7.0$  have greater weight of leaves, roots and rhizome, and the whole individuals ( $P < 0.0001$ ). The greatest increase is observed in the length of the roots ( $P < 0.0001$ ). A significant increase in the mass of the rhizome ( $0.02 \pm 0.01 \text{ g d.w.}$  against  $0.01 \pm 0.01 \text{ g d.w.}$ ) suggests that the lifetime of these individuals is probably longer than that of the individuals growing

in more acid waters. At the pH values from this range the fecundity of the species is the greatest ( $8.1 \pm 5.5$  flowers and fruits,  $P < 0.05$ ), which suggests that in weakly acid waters *Luronium natans* finds the optimum living conditions.

**In water of pH 7.1–8.0** the individuals are lighter, which is due to a decrease in the length of the roots ( $P < 0.0001$ ) because the weight of the leaves is at the same level as for the individuals from the group described above (Fig. 2). The contribution of the roots in the biomass of the whole individual is only 18% (while in the previous group is 31%; Table 4). It causes a significant increase in the ratio of the mass of the aboveground to that of the underground parts, from  $2.6 \pm 1.3$  to  $5.0 \pm 2.6$ ,  $P < 0.0001$ . The aboveground organs make as much as 82% of the mass of the individual, while in the previous group they make 69%; it resulted from a reduction of the

size of the roots and an increase in the assimilative area of the leaves. It should be emphasised that in weakly alkaline water the fecundity of *Luronium natans* is lower than in weakly acid water.

**In water of pH > 8.0**, the weight of the leaves, rhizome and the whole individual is smaller while that of the roots and their length do not change relative to those of the individuals from the previous group ( $P < 0.001$ ; Fig. 2, Table 3). The roots make 26%, the rhizome – 33%, and the leaves 41% of the mass of the individual. The aboveground and the underground organs take 74% and 26% of the mass of the individual, respectively. The main response of the plant to the environment conditions is a significant decrease in the assimilative area ( $P < 0.0001$ ). The reduction of the aboveground organs is statistically significant ( $P < 0.0001$ ), however, it is not accompanied by a decrease in the fecundity of individuals.

Table 3. Characters of *Luronium natans* related to pH, total phosphorus (TP) and DOC concentration in the water. Data from 21 lakes in North-Western Poland (July 2001, 2002; n – no. of individuals).

Character	No. of lakes	Area of rosette [cm <sup>2</sup> ]	Length of roots [cm]	No. of flowers and fruits	Aboveground weight [g d.w.]	Above/underground biomass ratio
<b>pH</b>		n=525	n=525	n=425	n=525	n=525
<5.0	2	17.4 ± 6.7	91.7 ± 45.1	3.8 ± 3.2	0.02 ± 0.01	2.2 ± 1.0
5.0–6.0	5	26.0 ± 12.4	123.6 ± 59.2	8.6 ± 5.9	0.03 ± 0.02	2.4 ± 1.0
6.1–7.0	6	30.9 ± 17.5	218.8 ± 107.0	8.1 ± 5.5	0.06 ± 0.03	2.6 ± 1.3
7.1–8.0	5	32.2 ± 18.3	125.7 ± 49.7	5.9 ± 4.4	0.06 ± 0.03	5.0 ± 2.6
>8.0	3	14.8 ± 9.1	122.6 ± 65.5	5.9 ± 6.3	0.04 ± 0.02	3.6 ± 2.2
<b>TP [μg dm<sup>-3</sup>]</b>		n=500	n=500	n=405	n=500	n=500
<10.0	1	15.7 ± 6.9	146.0 ± 88.1	6.0 ± 5.7	0.02 ± 0.01	1.8 ± 0.9
10.0–15.0	5	37.7 ± 21.4	118.8 ± 55.4	7.1 ± 3.9	0.05 ± 0.03	3.9 ± 2.9
15.1–20.0	5	32.3 ± 12.5	205.3 ± 117.9	6.2 ± 2.8	0.06 ± 0.02	3.3 ± 0.9
20.1–30.0	4	23.5 ± 14.5	168.2 ± 96.4	5.4 ± 4.9	0.04 ± 0.02	3.2 ± 2.0
>30.0	5	13.0 ± 8.2	115.7 ± 49.4	6.6 ± 5.4	0.04 ± 0.02	3.6 ± 2.1
<b>DOC [mg C dm<sup>-3</sup>]</b>		n=425	n=425	n=345	n=425	n=425
<3.5	3	29.0 ± 20.4	102.0 ± 37.2	5.5 ± 3.1	0.04 ± 0.03	2.5 ± 1.3
3.5–5.0	6	29.2 ± 16.6	133.1 ± 57.6	5.5 ± 4.7	0.05 ± 0.03	3.6 ± 2.4
5.1–6.0	3	29.7 ± 15.4	223.7 ± 123.5	7.6 ± 4.3	0.06 ± 0.03	3.0 ± 1.3
>6.0	5	17.5 ± 10.4	149.1 ± 86.8	12.3 ± 7.2	0.04 ± 0.02	3.1 ± 2.1

### 3.3. The effect of the total phosphorus concentration

**In water of TP < 10.0 μg dm<sup>-3</sup>**, the *Luronium natans* individuals are the smallest, the lightest and show low fecundity (Fig. 3). The aboveground organs take 61% of the mass of the individual, and of this amount 36% is allocated in leaves and 25% in the rhizome (Ta-

ble 4). The assimilative area of the rosette is very small ( $15.9 \pm 7.0$  cm<sup>2</sup>). The mass of the roots makes 39% of the whole mass of a plant. The proportion of the mass of the aboveground to the underground organs is low ( $1.8 \pm 0.9$ ). The arithmetic mean of the number of flowers and fruits is  $6.0 \pm 5.7$ , and is similar to that obtained for the individuals growing in the conditions of higher TP con-

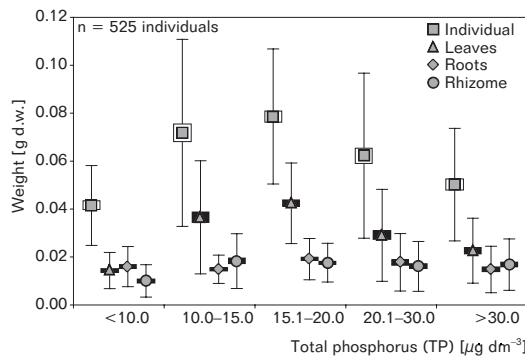


Fig. 3. Variation of the biomass of an individual plant, leaves, roots, rhizome in relationship to phosphorus concentration in the water (mean, standard error, range; No. of lakes see Table 3).

centrations. Thus, the difference in the number of flowers and fruits from the individuals from all groups distinguished with respect to TP is statistically insignificant.

**In water of TP 10.1–15.0  $\mu\text{g dm}^{-3}$ ,** the individuals of *Luronium natans* are greater and weight more ( $P < 0.001$ ) than those from the previous group, however, their fecundity does not change (Fig. 3, Table 3). In these conditions as much as 78% of the mass of the plant is allocated in the aboveground organs (an increase by 17%;  $P < 0.0001$ ). The weight of the leaves ( $P < 0.0001$ ) and the rhizome ( $P < 0.0001$ ) is greater. The leaves take 52% and the rhizome takes 26% of the mass of an individual, which causes a significant increase in the proportion of the mass of the aboveground to that of the underground organs ( $P < 0.0001$ ). The individuals of *Luronium natans* collected from water of TP from this range are the greatest, but their fecundity remains at the same level.

**In water of TP 15.1–20.0  $\mu\text{g dm}^{-3}$**  the individuals of *Luronium natans* are characterised by the same weight and fecundity as those from the previous group, ( $P > 0.05$ ), but have significantly smaller assimilative area ( $P < 0.0001$ ). The proportion of the mass of the aboveground to the underground organs is also lower.

**In water of TP 20.1–30.0  $\mu\text{g dm}^{-3}$**  the individuals of *Luronium natans* have lower weight ( $P < 0.001$ ) than those from the previous group, mainly because of a decrease in the weight of the leaves ( $P < 0.0001$ ) and the length of the roots (Fig. 3, Table 3). The assimilative area of the leaves also decreases ( $P < 0.001$ ). The aboveground organs take 71% of the total mass of an indi-

vidual, while in the plants of the previous group – 75%;  $P < 0.0001$ . Despite these changes in the plant properties, the fecundity remains at the same level.

**In water of TP  $> 30.1 \mu\text{g dm}^{-3}$**  the weight of the *Luronium natans* individuals decreases ( $P < 0.005$ ), mainly as a consequence of a significant decrease in the assimilative area ( $13.0 \pm 8.2 \text{ cm}^2$  against  $23.5 \pm 14.5 \text{ cm}^2$ ), and in the mass and the length of the roots (Fig. 3, Table 3). The weight of the rhizome and the fecundity of individuals remain at the same level. Analysis of the *Luronium natans* response to the TP concentration shows that the optimum conditions for the species development are at the TP concentration 10.1–20.0  $\mu\text{g dm}^{-3}$  (Fig. 3, Table 3).

### 3.4. The effect of DOC

**In water of DOC concentration  $< 3.5 \text{ mg C dm}^{-3}$ ,** i.e. in the presence of a small amount of allochthonous humic substances (and a small primary production), the *Luronium natans* individuals have large assimilative area, but a short and rather heavy root system (Table 3). The mass allocation is following: 47% to the leaves, 24% to the rhizome and 29% to the roots (Table 4). The arithmetic mean of the proportion of the mass of the aboveground to that of the underground parts is  $2.5 \pm 1.3$ , which means that 71% of the mass is allocated in the aboveground organs. An individual produces on average 5 flowers and fruits, however, the range of variation of the latter is wide (1–17; CV = 0.57).

**In water of DOC 3.5–5.0  $\text{mg C dm}^{-3}$**  the *Luronium natans* individuals are similar to those growing in water of DOC concentration  $< 3.5 \text{ mg C dm}^{-3}$ , that is no statistically significant differences in any of the traits studied have been found (Fig. 4, Table 3). Thus, it can be assumed that in water of DOC concentration up to 5  $\text{mg C dm}^{-3}$  the species does not show a significant response to this environmental factor.

**In water of DOC 5.1–6.0  $\text{mg C dm}^{-3}$**  the assimilative area of the rosette has a similar size but the weight of the individuals increases ( $P < 0.001$ ), mainly because of an increase in the leaves biomass. The weight of the rhizome is the same ( $0.02 \pm 0.01 \text{ g d.w.}$ ; Fig. 4), but the fecundity of the plant increases and the mean number of flowers and fruits per an individual is 7.

Table 4. Proportion (%) of leaves, rhizome, roots in individual biomass of *Luronium natans* in relation to pH, total phosphorus (TP), DOC concentration in the water (July 2001, 2002).

pH	<5.0	5.0–6.0	6.1–7.0	7.1–8.0	>8.0
Leaves	46	48	46	52	41
Rhizome	20	22	23	30	33
Roots	34	30	31	18	26
TP [ $\mu\text{g dm}^{-3}$ ]	<10.0	10.1–15.0	15.1–20.0	20.1–30.0	>30.1
Leaves	36	52	53	46	43
Rhizome	25	26	22	25	31
Roots	39	22	25	29	26
DOC [ $\text{mg C dm}^{-3}$ ]	<3.5	3.5–5.0	5.1–6.0	>6.0	
Leaves	47	50	54	35	
Rhizome	24	27	20	33	
Roots	29	23	26	32	

In water of DOC > 6.0 mg C dm<sup>-3</sup>, the individuals of *Luronium natans* have the smallest assimilative area (a decrease by 40%;  $P < 0.0001$ ). The length of the roots decreases ( $P < 0.0001$ ) as does the total mass of the plant ( $P < 0.0001$ ). The changes are mainly a consequence of a decrease in the weight of the leaves, as the weight of the roots and rhizome remain unchanged. In the conditions of the highest DOC concentration, mostly originating from allochthonous humic substances, the *Luronium natans* individuals have the smallest assimilative area but produce the greatest number of flowers and fruits ( $P < 0.0001$ ; Table 3).

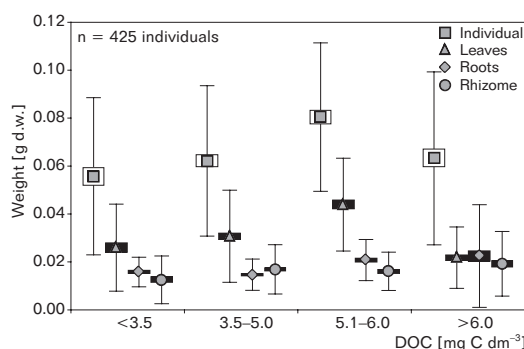


Fig. 4. Variation of the biomass of an individual plant, leaves, roots and rhizome in relationship to dissolved organic carbon (DOC) concentration in the water (mean, standard error; No. of lakes see Table 3).

#### 4. DISCUSSION

*Luronium natans* is an isoetids of the rosette type of growth, and hence, likewise other plants from this group, absorbs the

main pool of nutrients from the bottom sediment (Boston and Adams 1985, 1986, Boston *et al.* 1987, 1989) and not from water as do most of the macrophytes. Usually the bottom sediments are acid and thus nutrient deficient.

In acid type of bottom sediments the rosette type of growth in *Luronium natans* is stimulated (Szmeja 1994). It implies a number of metabolism characteristics (Wium-Andersen 1971, Boston *et al.* 1989) and the tendency of the species to occupy acid and nutrient deficient sites (Szmeja 1987a, b, Rørslett and Brettum 1989, Szmeja and Clément 1990). The rosette type of growth is an adaptive feature developed as a result of natural selection (Szmeja 1994). Changes in this form of growth can be a good comparative measure of the plant's response to the environmental conditions.

The main feature in the morphology of *Luronium natans* individuals is a great mass of the root system, and one of the main response of this species to the environmental conditions is a reduction of this system in the conditions of enhanced trophy of the lake; it suggests a significant role of this organ in absorption of resources directly from the sediments. The root system of *Luronium natans* individuals usually takes from 17% to 40% of the total mass of the individual (28% on average). It is characteristic for isoetids, e.g. *Lobelia dortmanna*, *Isoetes lacustris* and *Littorella uniflora*. In these species the root system takes from 26% to 31% of the total mass (Szmeja 1992). The type of bottom sediment is an important diagnostic feature for assessment of aquatic sites occupied by this species.

Like the majority of submerged plants, *Luronium natans* absorbs inorganic carbon for photosynthesis from  $\text{HCO}_3^-$  ions and additionally from free  $\text{CO}_2$ ; in specific conditions (pH > 9.0) also from  $\text{CO}_3^{2-}$  (Loczy *et al.* 1983, Boston *et al.* 1987). *Luronium natans* finds the optimum conditions of growth in water of poor buffer properties (pH 6.1–7.0). Both highly acid (pH < 5.0) and alkaline (pH > 8.0) water is unsuitable for this species as the concentration of  $\text{HCO}_3^-$  ions is very low in this kind of water. In other words pH changes beyond the range 6.1–7.0 are unfavourable for *Luronium natans*. The protection of this species should aim at preservation of the slightly acid-neutral character of the water and the bottom sediments of its environment, to enable the plant to use the inorganic carbon from  $\text{CO}_3^{2-}$  ions and free  $\text{CO}_2$ .

Frequently, pH changes of the lake water and bottom sediments are caused by the introduction of humus substances into the lakes. With increasing DOC concentration the lake water colour gets more intense, its conductivity and TN concentration increase, while the content of calcium decreases. In such conditions the size and fecundity of many rooted macrophytes decrease (Szmeja *et al.* 2001) as do those of *Luronium natans*. The plant prefers transparent water (< 20 mg Pt  $\text{dm}^{-3}$ ) and low DOC concentration (< 6.0 mg C  $\text{dm}^{-3}$ ). Higher concentration of this carbon species is harmful for the plant. The main response of *Luronium natans* to a growing concentration of DOC in water is an increase in the fecundity of individuals (Table 3, Fig. 4). The plant dies at DOC concentrations above 10.0 mg C  $\text{dm}^{-3}$ . These conditions also cause death of the other *Cormophyta*, some *Bryophyta* and almost all *Charales* (Szmeja 2000, Szmeja *et al.* 2001). With increasing DOC concentration in lake water the macrophytes-covered areas move towards shallow littoral, the frequency and the density of the plants decrease. Consequently, the population deteriorates mainly because of a decrease in of light attenuation (Szmeja and Bociąg in press).

*Luronium natans* prefers nutrient deficient waters of TP concentrations in the range 10.1–20.0  $\mu\text{g dm}^{-3}$  (Table 3). In lower TP concentrations (< 10.0  $\mu\text{ dm}^{-3}$ ) the individuals of this species are small and show low fecundity. The plant responds to an increase in TP concentrations in the

range from 10.0 to 20.0  $\mu\text{g dm}^{-3}$  positively i.e. the individuals' biomass and fecundity increase. However, an increase in TP concentration above 20.1  $\mu\text{g dm}^{-3}$  causes a negative response of the plant. In soft-water lakes of TP concentration above this value, the size and fecundity of the individuals decrease, which can partly be accounted for stronger competitive interactions with other macrophytes or filamentous algae. Another reason for this decrease could be a reduction of the intensity of light related to increasing primary production.

The changes in the morphology and fecundity of *Luronium natans*, caused by an increase in lake water acidity or trophic state are in general very similar in character. This observation suggests that the reason for dying out of *Luronium natans* can be the environment-induced changes within the plant, in particular those leading to a decrease in the size of the same-age individuals. All other responses of the plant are secondary to the decrease in the size (Szmeja 1992, Falińska 2002). The smaller size hinders the recruitment of offspring in populations (Szmeja 1994) and increases the rate of their death.

## 5. SUMMARY

The size, biomass allocation and fecundity of *Luronium natans* (L.) Raf. in plants collected from 21 lakes in the Pomeranian Lake District have been analysed (NW Poland; Fig. 1). The plant growth in low-productivity lakes whose water is characterised by the concentrations of DOC < 6 mg C  $\text{dm}^{-3}$ , calcium 1.3–18.4 mg Ca  $\text{dm}^{-3}$ , total phosphorus (TP) 7.8–56.4  $\mu\text{g dm}^{-3}$  and pH 4.5–8.5 (Table 1). The lake bottom sediment in the population areas is mainly mineral, usually acid (pH 4.2–7.4) and has a low content of calcium (0.9–3.2 mg Ca  $\text{g}^{-1}$  d.w.; Table 2). The greatest and most fecund individuals grow in slightly acid lakes (pH 6.1–7.0; Fig. 2, Table 3), poor in TP (10.0–20.0  $\mu\text{g dm}^{-3}$ ; Fig. 3, Table 3) and DOC (3.5–6.0 mg C  $\text{dm}^{-3}$ ; Fig. 4, Table 3). In the optimum living conditions the biomass is allocated as follows: 46–54% in the leaves, 22–31% in the roots, 20–27% in the rhizome (Table 4). In highly acid water (pH < 5.0) or in lakes of elevated trophic state (> 20.0  $\mu\text{g TP dm}^{-3}$ ) and a significant DOC concentration (> 6 mg C  $\text{dm}^{-3}$ ), a statistically significant decrease in the plant size is observed.

The main environmental factor leading to a decrease in the fecundity of *Luronium natans* individuals is acidification of lake water. Any change in pH of the lake water beyond the ran-

ge 6.1–7.0 are unfavourable for *Luronium natans*. The changes in the size and fecundity of *Luronium natans* induced by an increase in the lake water acidity or by an increase in the lake trophic state are similar. The main reason for dying out of *Luronium natans* is the environment-induced changes in the plant, especially those leading to a decrease in the size of the same-age individuals in the population. They lead to inhibition of the offspring recruitment in populations and to an increase in the death rate. The protection of *Luronium natans* should be aimed at preservation of the appropriate pH of the lake water and bottom sediments allowing the plant to use the inorganic carbon from  $\text{CO}_3^{2-}$  and free  $\text{CO}_2$ .

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## 6. REFERENCES

- Arts G. H. P., Den Hartog C. 1990 – Phyto-geographical aspects of the West European softwater macrophyte flora – *Acta Botanica Neerlandica* 39: 369–378.
- Boston H. L., Adams M. S. 1985 – Seasonal diurnal acid rhythms in two aquatic crassulacean acid metabolism plants – *Oecol.* 65: 573–579.
- Boston H. L., Adams M. S. 1986 – The contribution of crassulacean acid metabolism to the annual productivity of two aquatic vascular plants – *Oecol.* 68: 615–622.
- Boston H. L., Adams M. S., Madsen J. D. 1989 – Photosynthetic strategies and productivity in aquatic systems – *Aquat. Bot.* 34: 27–57.
- Boston H. L., Adams M. S., Pienkowski T. P. 1987 – Models of the use of root-zone  $\text{CO}_2$  by selected North American isoetids – *Ann. Bot.* 60: 485–494.
- Collier K. J. 1987 – Spectral properties of some West Coast waters and their relationship with dissolved organic carbon – *Mauri Ora* 14.
- Dąbwska I. 1965 – Roślinność litoralu jezior lobeliowych Pojezierza Kartuskiego – *PTPN, Prace Kom. Biol.* 30: 1–53. (in Polish)
- 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)
- 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)
- Greenberg A. E., Clesceri L. S., Eaton A. D. 1992 – Standard methods for the examination of the water and wastewater – American Public Health Association, 18<sup>th</sup> edition, Washington.
- 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)
- Hultén E., Fries M. 1986 – Atlas of north european vascular plants – Koeltz Scientific Books, Königstein, 1172 pp.
- Loczy S., Carignan R., Planas D. 1983 – The role of roots in carbon uptake by submersed macrophytes *Myriophyllum spicatum*, *Vallisneria americana* and *Heteranthis dubia* – *Hydrobiologia*, 98: 3–7.
- 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.
- Rørslett B., Brettum P. 1989 – The genus *Isoetes* in Scandinavia: an ecological review and perspectives – *Aquat. Bot.* 35: 223–261.
- Smits A. J. M., Laan P., Thier R. H., Van Der Velde G. 1990 – Root aerenchyma, oxygen leakage patterns and alcoholic fermentation ability of the roots of some nymphaeid and isoetid macrophytes in relation to the sediment type of their habitat – *Aquat. Bot.* 38: 3–17.
- Sokal R. R., Rohlf F. J. 1995 – *Biometry. The principles and practice of statistics in biological research. II Edition* – W. H. Freeman & Comp., New York.
- Szańkowski M., Kłosowski S. 2001 – Habitat conditions of the phytocoenoses dominated by *Luronium natans* (L.) Rafin in Poland – *Hydrobiologia* 455: 213–222.
- 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. I. The plasticity of individuals within a constant depth interval in oligotrophic lakes – *Ekol. pol.* 35: 497–522.
- Szmeja J. 1992 – Struktura, organizacja przestrzenna i demografia populacji isoetydów [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. Zukowski) – 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.*
- Szmeja J., Clément B. 1990 – Comparaison de la structure et du déterminisme des *Littorelletea uniflorae* en Poméranie (Pologne) et en Bretagne (France) – *Phytocoenologia*, 19: 123–148. (in French)
- Tennant D. 1975 – A test of modified line interest method of estimating root length – *J. Ecol.* 63: 995–1001.
- Weeda E. J., Westra R., Westra C., Westra T. 1991 – Nederlandse oecologische flora, deel 4 IVN (Dutch ecological flora) – VARA en Vewin, Amsterdam.
- Wium-Andersen S. 1971 – Photosynthetic uptake of free CO<sub>2</sub> by roots of *Lobelia dortmanna* – *Physiol. Plant* 252: 245–248.

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