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Autor: Woek, Jerzy

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Synusial assemblages of pleustonic plants of the genera *Lemna*, *Spirodela*, *Wolffia*, *Salvinia*, *Hydrocharis*, *Riccia* and *Ricciocarpus*

Jerzy WOŁEK

1. INTRODUCTION

As often demonstrated, assemblages of free floating water plants (= pleustonic plants) establish their synusiae within rush and aquatic vegetation (PANKIN 1947, LOHAMMAR 1965, HEJNY 1971, KEPZYNSKI 1972, REJMANKOVA 1975, PASSARGE 1978, FINTHA 1979, OCHYRA and TOMASZEWICZ 1979 and others). Besides a few scarce and general remarks, however, no more detailed data on the subject have as yet been published.

In this paper, the results of studies are represented on the occurrence of individual pleustonic plant species and their assemblages within different plant communities occurring in aquatic habitats.

2. MATERIAL AND METHODS

Nine pleustonic species were considered, including *Lemna minor* L., *L. trisulca* L., *L. gibba* L., *Spirodela polyrrhiza* (L.) Schleid., *Wolffia arrhiza* (L.) Wimm., *Salvinia natans* (L.) All., *Riccia fluitans* L., *Ricciocarpus natans* (L.) Corda and *Hydrocharis morsus-ranae* L. All but the last species are unanimously regarded as characteristic of the class *Lemnetae*. As to *Hydrocharis morsus-ranae*, opinions are divided, and more relevant information is to be found in WOŁEK (1983).

The study in question was carried out with phytosociological data which had already been used to study determinants of species composition in pleustonic assemblages (WOLEK 1983). In addition, use was made of synthetic tables worked out by TOMASZEWICZ (1980). Of the relevés collected by the present author, only those with a clearly defined syntaxonomic position were taken into account. In general, this study does not include relevés which are classed in the *Myriophyllo-Nupharetum* W. Koch 1926 and *Scirpo-Phragmitetum* W. Koch 1926 associations because latest findings show that phytocoenoses, included until recently in the two syntaxons mentioned above, represent different associations which often belong to separate alliances (TOMASZEWICZ 1973, 1977). Likewise, for obvious reasons, pleustonic associations, as well as *Hydrocharitetum morsus-ranae* van Langendonck 1935, were not considered in this paper. On the whole, 738 phytosociological records, selected from the author's collection, were used. This selection as well as the data taken from TOMASZEWICZ (1980) served as the basis for an inventory of all plant associations occurring in the aquatic habitats. All associations were registered in which even one of the above mentioned pleustonic species was found, regardless of its degree of abundance.

3. RESULTS

Based on the author's material, individual pleustonic species were found in 42 associations assembled in 12 alliances. These associations embrace aquatic and rush phytocoenoses as well as phytocoenoses of wet alderwood, therophytes, minor amphibian perennials and phytocoenoses which develop in both oligotrophic waters of fens and dystrophic waters of fens and raised bogs. On the basis of synthetic tables provided by TOMASZEWICZ (1980) the presence of pleustonic plants was demonstrated in 54 aquatic and rush associations classed into nine alliances. Considering 34 associations common in both cases, the total number of plant associations penetrated by pleustonic species amount to 64 associations assembled in 14 alliances. These associations are listed in Table 1 along with an indication of those pleustonic plant species that are encountered in them.

At first sight two distinct groups of species are easily recognizable, one including *Lemna minor*, *L. trisulca*, *Spirodela polyrrhiza* and *Hydrocharis morsus-ranae* and the other comprised of *Wolffia arrhiza*, *L. gibba*, *Salvinia natans*, *Riccia fluitans* and *Ricciocarpus natans*. Species of the first group recur fairly regularly in all associations of the aquatic and rush plants,

while species of the second group occur mainly in the associations of the alliances *Nymphaeion*, *Phragmition* and *Magnocaricion*. The latter species are missing entirely in associations of the alliance *Charion fragilis*. *L. minor*, *L. trisulca*, *S. polyrrhiza* and *Hydrocharis morsus-ranae* penetrate, respectively, 49, 50, 36 and 43 plant associations, on average 44.5 associations. On the other hand, *W. arrhiza*, *L. gibba*, *S. natans*, *R. fluitans* and *R. natans* penetrate, respectively, 7, 8, 8, 12 and 8 plant associations, on the average 8.6 associations. In sum, species of the first group penetrate five times as many associations as do species of the second group. What is surprising here, is how negligible the differences are between species within each group in regards to the penetrated associations as shown in Table 1, and in this respect, how the boundary is marked between species belonging to separate groups.

The occurrence of pleustonic assemblages in plant associations occurring in aquatic habitats was determined on the basis of the author's relevés (Table 2), because synthetic tables prepared by TOMASZEWICZ (1980) were not appropriate for this purpose. Individual associations in the sample were, for the most part, represented in a small number of relevés, they were therefore presented in the form of plant alliances.

In Table 2, the fractions of relevés containing 1 to 7 pleustonic species as related to plant alliances are presented. The fractions are not given in the form of relative numbers because of the generally small size of samples ($N < 50$). For the same reason, distributions shown in Table 2 are not quite suitable for a detailed statistical analysis. Fairly credible conclusions concerning the occurrence frequency of k-species combinations can be made in the cases of *Magnocaricion* and *Phragmition* because only in these cases sufficient numbers of relevés exist (Table 2). Since the observed distributions of relevés, characteristic of both these alliances, show a fairly good agreement, both samples of relevés were combined and the fractions of relevés that fall into each category of random variable, k, were calculated for such a general sample. The greatest number of relevés, i.e. 46.6%, contained one-species pleustonic assemblages. Two-species assemblages were found in 32.8% of the relevés, those of 3-species in 15.8%, 4-species assemblages were present in 3.7%, and 5-species in 1% of the relevés. Consistently, in the alliances *Magnocaricion* and *Phragmition* there occur mainly assemblages composed of a small number of pleustonic species, multi-species assemblages being extremely rare. It is supposed that the frequency distribution of k-species pleustonic assemblages in the remaining alliances is probably the same as in the case of *Magnocaricion* and *Phragmition* alliances. It is probably possible to

Table 1. Occurrence of *Lemna minor* (1), *L. trisulca* (2), *Spirodela polyrrhiza* (3), *Hydrocharis morsus-ranae* (4), *Wolffia arrhiza* (5), *Lemna gibba* (6), *Salvinia natans* (7), *Riccia fluitans* (8), and *Ricciocarpus natans* (9) in plant associations occurring in aquatic habitats. Syntaxonomy of the associations according to TOMASZEWICZ (1980) and MATUSZ-KIEWICZ (1981).

Class Order Alliance Association	Species								
	1	2	3	4	5	6	7	8	9
Charetea Fukarek 1961									
Charetalia Sauer 1937									
Charion fragilis Krausch 1964									
Nitellopsidetum obtusae (Sauer 1937) Dąbbska 1961		x							
Charetum fragilis Fijałkowski 1960	x		x						
Charetum contrariae Corillion 1957	x	x							
Charetum jubatae Krausch 1964			x						
Charetum rudis Dąbbska 1966			x						
Charetum aculeolatae (Corillion 1957) Dąbbska 1966	x				x				
Charetum vulgaris Corillion 1957	x	x							
Charetum coronatae Corillion 1957			x	x					
Charetum hispidae Corillion 1957	x	x		x					
Charetum strigosae Dąbbska 1966	x								
Nitellion Dąbbska 1966									
zbiornisko z Nitella mucronata	x								
Potamogetonetea R. Tx. et Preisg. 1942									
Potamogetonalia W. Koch 1926									
Potamogetonion (W. Koch 1926) Oberd. 1957									
Potamogetonetum lucentis Hueck 1931	x	x	x	x					
Potamogetonetum perfoliatum (W. Koch 1926) Pass. 1964			x						
Potamogetonetum pectinatum Carstensen 1955	x	x		x					
Myriophylletum verticillatum Soó 1927	x	x	x	x				x	
Myriophylletum spicatum Soó 1927	x		x						
Ranunculetum circinatum (Bennema et Westh. 1943) Segal 1965	x	x							
Elodeetum canadensis (Pign. 1953) Pass. 1964	x	x	x	x			x	x	
Ceratophylletum demersi Mild 1965	x	x	x	x					
Potamogetonetum obtusifolium (Carstensen 1954) Segal 1965		x	x	x					
Parvopotamogetoneto-Zannichelietum W. Koch 1926		x							
Potamogetonetum filiformis W. Koch 1926	x			x					
Potamogetonetum mucronatum Tomaszewicz 1980		x							
Nymphaeion W. Koch 1926									
Nuphareto-Nymphaeetum albae Tomaszewicz 1977	x	x	x	x					
Nymphaeetum candidae Miljan 1958	x	x	x	x					
Nupharetum pumili Oberd. 1957		x							
Trapetum natantis Müller et Görs 1960	x	x	x	x	x	x	x	x	
Nymphoidetum peltatae (All. 1922) Oberd. et Müller 1960	x	x	x	x			x	x	x
Potamogetonetum natantis Soó 1927	x	x	x	x		x	x	x	
Polygonetum natantis Soó 1927		x							
Hottonion Segal 1964									
Hottonietum palustris R. Tx. 1937	x	x	x	x				x	x
Phragmitetea R. Tx. et Preisg. 1942									
Phragmitetalia W. Koch 1926									
Phragmition W. Koch 1926									
Scirpetum lacustris (All. 1922) Chouard 1924	x	x	x	x					
Typhetum angustifoliae (All. 1922) Soó 1927	x	x	x	x	x				
Phragmitetum (Gams 1927) Schmale 1939	x	x	x	x					
Equisetum limosi Steffen 1931	x	x	x	x				x	x

Table 1 (continued)

Class Order Alliance Association	Species								
	1	2	3	4	5	6	7	8	9
Typhetum latifoliae Soó 1927	x	x	x	x	x	x		x	x
Sparganietum erecti Roll 1938	x	x	x	x					
Glycerietum maximae Hueck 1931	x	x	x	x		x		x	x
Acoretum calami Kobendza 1948	x	x	x	x		x			
Scirpetum maritimi (Christ. 1934) R. Tx. 1937	x	x	x						
Oenanthero-Rorippetum Lohm. 1950	x	x	x	x	x				
Cladietum marisci (All. 1922) Zobr. 1935					x				
Thelypteridi-Phragmitetum Kuiper 1957	x	x		x					
Eleocharido-Sagittarion Pass. 1964									
Eleocharitetum palustris Schennikow 1919	x	x	x	x					
Sagittario-Sparganietum R. Tx. 1953	x	x	x	x			x		
Hippuridetum vulgaris Pass. 1955	x	x		x					
Sparganio-Glycerion Br.-Bl. et Siss. 1942									
Sparganio-Glycerietum fluitantis Br.-Bl. 1925	x		x						
Glycerietum plicatae Oberd. 1957	x	x							
Magnocaricetalia Pign. 1953									
Magnocaricion W. Koch 1926									
Phalaridetum arundinaceae Libb. 1931	x								
Caricetum gracilis (Graebn. et Hueck 1931) R. Tx. 1937	x	x	x	x		x	x		x
Caricetum acutiformis Sauer 1937	x	x	x	x					
Caricetum ripariae Soó 1928	x	x	x	x					
Caricetum elatae W. Koch 1926	x	x	x	x				x	x
Caricetum rostratae Rüb. 1912	x	x	x	x				x	x
Caricetum paniculatae Wang. 1916	x	x	x	x	x		x	x	
Caricetum vesicariae Br.-Bl. et Denis 1926	x	x	x	x					
Iretum pseudoacori Egger 1933 nom. nud.	x	x	x	x	x	x			
Cicuto-Caricetum pseudocyperii de Boer 1942	x	x	x	x	x				
Caricetum distichae (Nowiński 1928) Jonas 1933					x				
Bidentetea tripartiti R. Tx., Lohm. et Preisg. 1950									
Bidentetalia tripartiti Br.-Bl. et R. Tx. 1943									
Bidention tripartiti Nordh. 1940									
Polygono-Bidentetum (W. Koch 1926) Lohm. 1950	x	x							
Utricularietea intermedio-minoris Den Hartog et Segal 1964 em. Pietsch 1965									
Utricularietalia intermedio-minoris Pietsch 1965									
Sphagno-Utricularion Müller et Görs 1960									
Sparganietum minimi Schaaf 1925	x	x		x				x	
Littorelletea uniflorae Br.-Bl. et R. Tx. 1943									
Littorelletalia uniflorae W. Koch 1926									
Eleocharition acicularis Pietsch 1966 em. Dierss. 1975									
Eleocharitetum acicularis (Baumann 1911) W. Koch 1926								x	
Scheuchzerio-Caricetea (Nordh. 1937) R. Tx. 1937									
Caricetalia fuscae W. Koch 1926 em. Nordh. 1937									
Caricion fuscae W. Koch 1926 em. Klika 1934									
Carici-Agrostietum caninae R. Tx. 1937					x				
Alnetea glutinosae Br.-Bl. et R. Tx. 1943									
Alnetalia glutinosae R. Tx. 1937									
Alnion glutinosae (Malc. 1929) Meijer Drees 1936									
Carici elongatae-Alnetum W. Koch 1926					x				

Table 2. Occurrence of pleustonic assemblages in different alliances of plant associations of aquatic habitats. The Table was prepared on the basis of 738 relevés selected from the author's collection.

N = number of relevés in a sample, k = number of pleustonic species in a relevé

Alliance	N	k						
		1	2	3	4	5	6	7
<i>Eleocharis acicularis</i>	1	1						
<i>Caricion fuscae</i>	1	1						
<i>Alnion glutinosae</i>	2	2						
<i>Bidention tripartiti</i>	6	4	2					
<i>Charion fragilis</i>	7	5	1	1				
<i>Eleocharido-Sagittarion</i>	19	4	6	8	1			
<i>Sphagno-Utricularion</i>	22	12	7	2	1			
<i>Hottonion</i>	47	12	13	10	12			
<i>Potamogetion</i>	43	20	10	6	6	1		
<i>Magnocaricion</i>	234	117	73	34	9	1		
<i>Phragmition</i>	302	133	103	51	11	4		
<i>Nymphaeion</i>	51	10	8	7	13	11	1	1

demonstrate this thesis by means of an adequately large sample of relevés. As it follows from Table 2, the plant alliances in question may be ordered in regards to the maximal number of pleustonic species observed in an assemblage in a given alliance. As it may be seen, one-species pleustonic assemblages occur in the associations of the alliances *Eleocharition acicularis*, *Caricion fuscae* and *Alnion glutinosae*, those of 1-2-species occur in associations of the alliance *Bidention tripartiti*, those of 1-3-species in associations of the alliance *Charion fragilis*, those of 1-4-species in associations of the alliances *Eleocharido-Sagittarion*, *Sphagno-Utricularion* and *Hottonion*, 1-5-species in associations of the alliances *Potamogetonion*, *Magnocaricion* and *Phragmition*, and 1-7-species in associations of the alliance *Nymphaeion*. Thus it may seem that when passing from the habitats of the alliance *Eleocharition acicularis* to those of the alliance *Nymphaeion*, the pleustonic assemblages find increasingly more suitable living conditions. However, there is an obvious correlation between the maximal number of species in a pleustonic assemblage and the sample size: the more numerous the relevés representing a given alliance, the higher the number of pleustonic species that are encountered in them. The foregoing methodical consideration should be taken into account when examining the influence that different habitats (symbolized by the individual alliances) may exert on the formation of a definite pleustonic assemblage. On the other hand, it cannot be excluded that the small number

of species in a pleustonic assemblage may result from the habitat influence. At the moment, it would be difficult to resolve these doubts due to a scarcity of factographical material.

4. DISCUSSION

The results obtained so far suggest that the species under study may be divided into two groups. Species of the first group (*L. minor*, *L. trisulca*, *S. polyrrhiza* and *H. morsus-ranae*) penetrate 5 times as many plant associations occurring in aquatic habitats as do the remaining species that belong to the second group. Such an effect could be explained based on the following hypotheses: 1) the null hypothesis assuming that species have identical habitat requirements and that they are dispersed independently of each other (= randomly); 2) the hypothesis assuming that species composition of pleustonic synusium depends mainly on the abiotic factors of habitat (species have different requirements as to the abiotic conditions of habitat and are independent of each other); 3) the hypothesis that species composition of pleustonic synusium depends on biotic factors, mainly on competition between the pleustonic species (species are not independent of each other).

In support of the first hypothesis the fact may be quoted that species of the first group are more common (= more probable) than the species of the second group (Table 3). The occurrence probabilities of the species belonging to the first group are markedly higher than those of the species belonging to the second group, but within each group the occurrence probabilities are very

Table 3. Occurrence probabilities of species under study, estimated on the basis of 1945 relevés (according to WOLEK 1983).

Species	Frequency	Fraction
<i>Lemna minor</i>	1424	0.293
<i>Lemna trisulca</i>	1080	0.223
<i>Spirodela polyrrhiza</i>	879	0.181
<i>Hydrocharis morsus-ranae</i>	820	0.169
<i>Wolffia arrhiza</i>	221	0.046
<i>Lemna gibba</i>	154	0.032
<i>Salvinia natans</i>	137	0.028
<i>Riccia fluitans</i>	97	0.020
<i>Ricciocarpus natans</i>	41	0.008
Total	4853	1.000

similar. If only to assume that the species in question disperse independently of each other (= randomly), that very fact may cause the natural isolation of both groups, i.e. species of the first group will be encountered in a greater number of plant associations than species of the second group. On the other hand, it may as well be admitted that the results obtained testify to the similar habitat requirements shown by the species within each of the distinguished groups, and testify to the fact that species of the first group have a broader ecological scale as compared with that of species of the second group. As frequently demonstrated (LANDOLT 1986), however, the observed differences in species composition of pleustonic synusia may be sufficiently explained by the varying requirements of the studied species as to the habitat abiotic conditions. Therefore, in the present author's opinion, there is no need for interpreting the analysed data in terms of an interspecific competition. According to the author's opinion, the null hypothesis and the one stressing role of the habitat abiotic conditions do not necessarily exclude each other but may be of a complementary character.

The list of plant associations presented above, providing habitats for pleustonic assemblages, is not yet complete. Further studies will certainly contribute to its completion in many aspects. Among other things, they will enable an explanation of the gaps in the occurrence of certain species in some plant associations occurring in aquatic habitat. For example, it seems hardly probable that the associations, in which one of the following species occurs, could be devoid of the remaining group members: *L. minor*, *L. trisulca*, *S. polyrrhiza* or *H. morsus-ranae*. From earlier studies (WOLEK 1983), it follows that combinations of these species are among the most common under natural conditions in Poland. Therefore, it seems that the absence of one of the above species in a given combination within an association of aquatic and rush vegetation is a matter of chance rather than of ecological conditions. However, the latter possibility cannot be entirely excluded. The results of studies by McLAY (1974) attested to this. It also seems possible that further detailed investigations could provide more credible information on the distribution of *W. arrhiza*, *L. gibba*, *S. natans*, *R. fluitans* and *R. natans*. In view of their small size (*W. arrhiza* and *R. fluitans*) or morphological differentiation (*L. gibba* and *R. natans*), some of these species can easily be overlooked, particularly if they are not especially sought after.

It would be interesting to analyse the collected material in detail. Such an analysis should consider the occurrence frequency of individual pleustonic species in different associations, particularly in aquatic and rush associations.

It should also consider the occurrence frequency of definite pleustonic assemblages in these associations. Valuable information on ecology of pleustonic plants and of their assemblages could thus be provided. Unfortunately, the available material has so far permitted only the superficial treatment of the subject. It seems, however, that the results obtained constitute a good starting point for further systematic investigations.

SUMMARY

The paper presents the results of a study on the occurrence of nine pleustonic species in different plant associations growing in aquatic habitats in Poland. Plants of the genera *Lemna*, *Spirodela*, *Wolffia*, *Salvinia*, *Hydrocharis*, *Riccia* and *Ricciocarpus* were taken into account. The study was based on relevés that already have been applied for studying determinants of species composition in pleustonic assemblages (WOLEK 1983). In addition, use was made of synthetic tables worked out by TOMASZEWICZ (1980). Individual pleustonic species were found in 64 plant associations of aquatic habitats, assembled in 14 alliances (Table 1). *Lemna minor*, *L. trisulca*, *Spirodela polyrrhiza* and *Hydrocharis morsus-ranae* penetrate respectively, 49, 50, 36 and 43 associations (an average of 44.5 associations), *Wolffia arrhiza*, *L. gibba*, *Salvinia natans*, *Riccia fluitans* and *Ricciocarpus natans* were found in respectively, 7, 8, 8, 12 and 8 associations (an average of 8.6 associations). In sum, species of the first group penetrate 5 times as many associations as do species of the second group. The occurrence of pleustonic assemblages in plant communities of aquatic habitats is presented in Table 2. Single-species pleustonic assemblages were found in associations of the alliances *Eleocharition acicularis*, *Caricion fuscae* and *Alnion glutinosae*, those of 1-2 species in association of the alliance *Bidention tripartiti*, those of 1-3 species in associations of the alliance *Charion fragilis*, those of 1-4 species in associations of the alliances *Eleocharido-Sagittarion*, *Sphagno-Utricularion* and *Hottonion*, those of 1-5 species in associations of the alliances *Potamogetonion*, *Magnocaricion* and *Phragmition*, and assemblages of 1-7 species in associations of the alliance *Nymphaeion*. The results were interpreted from the viewpoint of three main hypotheses: 1) the null hypothesis (species have identical habitat requirements and disperse independently of each other, i.e. randomly); 2) the hypothesis that species composition of a pleustonic synusium depends on abiotic factors (species have different requirements as to abiotic factors of the habitat and are independent of each other); 3) the hypothesis that species composition of a pleustonic synusium depends on biotic factors, mainly on competition between pleustonic species (species are not independent of each other). According to the author's opinion, differences in species composition of the pleustonic synusiae under study can be sufficiently explained on assuming that species disperse randomly and that their distribution is influenced by the habitat's abiotic factors.

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Address of the author: Dr. Jerzy WOLEK
Polish Academy of Sciences
Wladyslaw Szafer Institute of Botany
Lubicz 46
PL-31512 Cracow