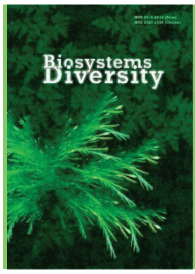

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Application of hemeroby and naturalness indicators for monitoring the aquatic macrophyte communities in protected areas

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The article discusses the application of hemeroby and naturalness indicators for monitoring the state of aquatic macrophytes in protected areas, taking into account the ecological characteristics of plant community syntaxons. Naturalness and hemeroby are considered as potential indicators of the state of aquatic ecosystems and the level of their anthropogenic transformation. Naturalness indicates the proximity of the community to the most natural state, and hemeroby indicates the level of anthropogenic transformation of the ecosystem. The vegetation cover of macrophytic communities of the "Dnipro-Orilskiy" Nature Reserve is represented by eight associations. Their differentiation is due to natural factors and factors caused by anthropogenic impact. The recorded plant communities demonstrate a compact spatial distribution. The *Nymphaeo albae-Nupharetum luteae* community occurs in the Dnipro riverbed. The *Ceratophyllo-Hydrocharitetum* associations were typical of the Orilsky Canal water bodies and were also found in Lake Sokilky, which is part of the Mykolaivka ledge system. The association's communities are common in the middle and lower reaches of the Dnipro. They are widespread in non-flowing water bodies with poor water exchange, neutral or slightly alkaline reaction of the environment in habitats protected from the wind, with water depth up to 50 cm, silted bottom sediments with a significant thickness of detritus and water transparency up to 15 cm. They are found in water bodies with excessive anthropogenic eutrophication processes. The *Typhetum latifoliae* association occurs in the system of the Obukhivka ledge system. The *Salvinio-Hydrocharitetum* association occurs mainly in the water bodies of the Taromske ledge system. The *Hydrocharito-Stratiotetum aloidis* association occurs in the water bodies of the Mykolaivka ledge system adjacent to the first floodplain terrace of the Dnipro. The *Lemno-Hydrocharitetum morsus-ranae* association is found in the streams of the Mykolaivka ledge system. The *Myriophylletum spicati* association occurs in the bays of the Mykolaivka ledge system, which directly border the Dnipro riverbed. The *Trapetum natantis* association occurs in the water bodies of the Mykolaivka and Taromske ledge system. The close spatial relationship of macrophyte associations with geomorphic areas of the Dnipro floodplain can help reconstruct the events that led to the current appearance of plant communities. It has been shown that the morphology of water bodies and their water properties largely determine the spatial distribution of aquatic macrophytes. The study has shown that climate continentality is an important differentiating factor that determines the characteristics of the vegetation cover of aquatic macrophytes. The *Typhetum latifoliae* association differs from others by the dominance of plants with a range that is widespread in Eastern Europe. This association is found in the water bodies of the Obukhivka ledge system, where specific environmental conditions are formed. These include significantly higher water salinity, shallow water that warms up well, and relatively high nutrient supply. It is also worth noting the low naturalness, which can be explained by the high level of coastal erosion, which causes secondary vegetation succession. The decrease in naturalness may be the result of increased secondary succession. The high level of naturalness of the communities indicates the role of the protected area regime in the conservation of biodiversity. However, the protected area regime alone cannot protect the reserve from the impact of a complex of anthropogenic factors. The anthropogenic transformation of plant communities is caused by eutrophication, which depends on both the availability of excessive nutrients and water temperature. Refugia of the rheophilic regime in the Dnipro floodplain form biodiversity centers that are highly natural and have significant conservation value. Indicators of naturalness and hemeroby are sensitive markers of the state of plant communities that can be used in the practice of biological monitoring in protected areas.

Keywords: nature protection; innovative projects; monitoring; bioindication; environmental impact assessment.

Introduction

Floodplains make a significant contribution to the conservation of freshwater biodiversity due to the variety of habitat types and features (Lukács et al., 2015). The floodplains of the great rivers of the European continent are negatively affected by the construction of dams (Hein et al., 2016), which catastrophically changes the water regime of rivers through the formation of reservoirs (Lin, 2011). The rheophilic regime of rivers is altered to a limnophilic regime. The loss of rheophilic habitats is of great significance for lowland rivers (Birnie-Gauvin et al., 2017). Flooding practically disappears as an element of the water regime of rivers after the construction of dams and regulated water flow, and at the same time, the ability of rivers to self-purify significantly deteriorates (Ahn, 2013). Under natural water regime conditions, floodplain reservoirs were connected to the riverbed only during high water, and the rest of the time they existed separately (Zhukov et al., 2024). Under regulated flow conditions, part of the floodplain reservoirs simply disappear, while the other part remains in contact with the riverbed all year round. It should be noted that riverbed water is a source of toxic substances and excessive nutrients that stimulate eutrophication (Hayes et al., 2018). In combination with a decrease in the potential for self-purification, this creates conditions for negative transformations in the structure of floodplain ecosystems. Floodplain ecosystems are a sensitive indicator of the state of ecosystems within the entire catchment area (Thoms, 2003).

Floodplain ecosystems are also a hotspot of biodiversity of terrestrial and aquatic communities (Schindler et al., 2016). These complexes perform important ecosystem functions that ensure the sustainable functioning of ecosystems over a large area. The functions and resilience of ecosystems depend on their diversity (Holmlund & Hammer, 1999), which is a pragmatic reason for conserving biodiversity (Niesenbaum, 2019). Biodiversity conservation has long been a component of environmental management, which requires the attraction of certain financial resources or justification for the involvement of land resources as objects of the nature reserve fund (Laurila-Pant et al., 2015). Floodplain and coastal lands have a high market value, and the creation of biodiversity reserves on their basis should be based on convincing arguments for the community (Chandra-Putra & Andrews, 2020). In other words, the development of tools and indicators of the dynamics of ecosystems during their protection is a relevant area of environmental procedures, which is a prerequisite for effective management. Obviously, such indicators should be sensitive, relevant, and understandable to decision makers and the community, but also based on key environmental phenomena and processes.

We aim to consider naturalness and hemeroby as potential indicators of the state of aquatic ecosystems and the level of their anthropogenic transformation. Naturalness indicates the closeness of the community to the most natural state (Angermeier, 2000), and hemeroby indicates the level of anthropogenic transformation of the ecosystem (Rüdisser et al., 2012). These indicators are usually seen as opposite: a distance from the natural state is a consequence of increased anthropogenic disturbance of ecosystems (Erdős et al., 2022). The assessment of hemeroby and naturalness is based on different principles. The naturalness indicator is a development of the concept of ecological strategies of plants according to Grime (2001) taking into account the conservation status of species or the potential for uncontrolled spread in the case of adventive plant species. This approach to assessing the naturalness indicator makes it sensitive to characterizing the state of ecosystems under conditions of a low level of anthropogenic transformation. Hemeroby is a variant of the phytoindication and is determined on the basis of expert judgment (Fehrenbach et al., 2015). The concept of hemeroby is based on the assumption that anthropogenic transformation is a consequence of complex environmental changes caused by human activity (Hill et al., 2002). The actual number of human-induced changes cannot be accurately accounted for, so anthropogenic transformation is considered as a holistic complex factor that can be measured only on the basis of the nonspecific response of plant species, which is reflected in the concept of hemeroby (Scown et al., 2016). It is natural that the hemeroby indicator is more sensitive to the dynamics of ecosystems that are under high levels of anthropogenic transformation. Thus, the combined use of hemeroby and naturalness allows the assessment of ecosystems in a wide range of levels of anthropogenic transformation. The use of the naturalness indicator is more appropriate for assessing the state of biota in nature reserves. However, it should be borne in mind that some factors of anthropogenic transformation of nature can spread significantly and negatively affect even protected areas. Therefore, the hemeroby indicator is also important for monitoring the state of protected ecosystems.

The syntaxonomic classification of vegetation is a common tool for studying the biodiversity of plant complexes (Mucina, 1997). The classification of habitats is also based on syntaxonomic method (Didukh et al., 2016). In turn, the habitat paradigm is the basis of modern conservation approaches (Prober et al., 2019). Therefore, the purpose of our article is to prove the use of hemeroby and naturalness indicators for monitoring the state of aquatic macrophytes in protected areas, taking into account the ecological features of plant community syntaxons.

Materials and methods

The research was performed in the summer of 2023 within the water bodies of the “Dnipro-Orilskiy" Nature Reserve (Dnipropetrovska Oblast, Ukraine). The "Dnipro-Orilskiy" Nature Reserve was created in 1990. The area is 3,766 hectares. The water bodies of the Reserve are situated within the Dnipro Reservoir, which is part of the cascade of reservoirs of the Dnipro River. The area of water bodies within the Reserve is 602.8 hectares. The database of recorded water bodies in the Reserve includes 302 objects. The water bodies can be divided into the following water systems: the Dnipro riverbed (total area of 223.4 ha), the Obukhivka ledge system (73.3 ha), the Orilsky Canal (21.7 ha), the Taromske ledge system (183.4 ha), and the Mykolaivka ledge system (101.0 ha).

The electrical conductivity, temperature, water transparency and dissolved oxygen content were measured at 291 monitoring points on 5, 6 and 7 August 2023. This period corresponds to the seasonal peak of temperatures, during which hypoxic crisis phenomena are most likely to occur in water bodies (Zhukov et al., 2024). The measurements were taken between 11 a.m. and 1 p.m., when the daily temperature variation was at its lowest. This period was selected because it represents the closest approximation to the maximum daily temperatures. The electrical conductivity of the water was measured using a portable water conductivity meter (HI 993310). The dissolved oxygen content was measured using a Hanna HI 98193 oximeter. The water transparency was measured using a Secchi disc. In floodplains, sand hills are of alluvial origin (Yakovenko et al., 2023): thus, the distance of the water body to the nearest sand hills can be considered a proxy for the intensity of alluvial processes. The distance of the water body boundary from the nearest Arenosols (sand hills) is derived from the study by Tutova et al. (2023).

The submerged, floating and emergent vegetation of all water bodies was surveyed in August 2023. The field survey procedure included the use of the strip transect method (Kolada et al., 2014). The method consists of observing the aquatic vegetation along 20 m wide strips perpendicular to the shoreline, covering the entire vegetation zone from the upper eulittoral to the outer limit of macrophyte growth. Observations were made by wading and by boat using a rake and a bathyscope. At each site, the maximum depth of cover and the average plant cover were determined and all submerged, floating and emergent plants were identified. The community matrix for the hydrobotanical relevés included 79 taxa recorded at 291 monitoring stations. Plant taxonomy was based on the Euro+Med Plantbase (http://ww2.bgbm.org/EuroPlusMed). The hemeroby values are given according to Frank Klotz (Frank & Klotz, 1990) with adaptation to regional conditions by Goncharenko (Goncharenko, 2017). The naturalness values of macrophyte species are given according to Borhidi (1995) with our adaptation to the conservation status of species and the potential for the spread of adventitious species in the region. The classification of anthropogenic impacts on ecosystems and the corresponding degrees of hemeroby and naturalness is based on Sukopp (1976), as amended by Podpriatova et al. (2023).

Phytocoenoses were distinguished using the TWINSPAN method of two-factor indicator species analysis (Davies & Grimes, 1999). Diagnostic syntaxon species were determined according to the values of the phi fidelity coefficient (Chytrý et al., 2002). Since this coefficient depends on the ratio of the number of descriptions of a particular phytocoenosis to the total number of descriptions involved in the analysis, we levelled the groups of descriptions. The statistical reliability of the coefficient was determined by Fisher's accuracy criterion at $P < 0.001$.

Results

Classification scheme of aquatic vegetation in the “Dnipro-Orilskiy" Nature Reserve.

- Class *Phragmito-Magnocaricetea* Klika in Klika et Novák 1941
  - Order *Phragmitetalia* Koch 1926
    - Union *Phragmition communis* Koch 1926
      - Association *Typhetum latifoliae* Nowiński 1930
- Class *Lemnetea* O. De Bolòs et Masclans 1955
  - Order *Lemnetalia minoris* O. de Bolòs et Masclans 1955
    - Union *Stratiotion* Den Hartog et Segal 1964
      - Association *Ceratophyllo-Hydrocharitetum* Pop 1962
      - Association *Lemno-Hydrocharitetum morsus-ranae* Oberd. 1957
      - Association *Hydrocharito-Stratiotetum aloidis* (van Langendonck 1935) Westhoff in Westhoff et Den Held 1969
      - Association *Salvinio-Hydrocharitetum* (Oberd. 1957) Boşcaiu 1966
- Class *Potamogetonetea* Klika in Klika et Novák 1941
  - Order *Potamogetonetalia* Koch 1926

Union *Nymphaeion albae* Oberd. 1957
Association *Trapetum natantis* Kárpáti 1963
Association *Nymphaeo albae-Nupharetum luteae* Nowiński 1927
Association *Myriophylletum spicati* Soó 1927

The association *Typhetum latifoliae* Nowiński 1930 included 33 plant species. On average, 15.0 ± 6.5 species were found on each survey plot (ranging from 11 to 20 species). The total projective cover varied from 86% to 100%. The Shannon diversity of the communities was 3.0 ± 0.1 bits/species (varied from 2.5 to 3.7 bits/species). The dominant species were *Phragmites australis* (Cav.) Trin. ex Steud. (projective cover 3–70%), *Typha latifolia* L. (0–45%), *Ceratophyllum demersum* L. (2–50%), *Mentha aquatica* L. (0–22%), *Typha angustifolia* L. (1–25%), and *Salvinia natans* (L.) All. (0–25%). The index of naturalness of this association was 3.1 ± 0.3 (in the range of 2.1 to 4.2). The index of hemeroby of this association was 41.0 ± 5.7% (in the range from 37.0% to 49.0%). The association prefers water with an electrical conductivity of 0.95 ± 0.06 dS/m (in the range of 0.52 to 1.35 dS/m), a temperature of 27.9 ± 2.0 °C (in the range of 24.5 to 29.9 °C), and an oxygen content of 12.2 ± 10.5 mg/L (in the range of 7.3 to 23.3 mg/L). The water transparency in the locations where this association occurs is 0.8 ± 0.1 meters (in the range from 0.4 to 1.3 m). The phytoindication assessment of the light regime indicates a value of 7.0 ± 0.02 (in the range from 6.8 to 7.2). The temperature regime had a score of 4.8 ± 0.01 (in the range from 4.6 to 5.0). The continentality regime had a score of 8.9 ± 0.01 (in the range from 8.5 to 9.0). The humidity regime had a score of 8.0 ± 0.02 (in the range from 7.7 to 8.4). The acidity regime had a score of 6.8 ± 0.01 (in the range from 6.7 to 7.0). Nutrients availability had a score of 6.8 ± 0.05 (in the range from 6.4 to 7.2).

The association *Ceratophyllo-Hydrocharitetum* Pop 1962 included 44 plant species. On average, 14.5 ± 15.2 species were found on each survey plot (ranging from 9 to 24 species). The total projective cover varied from 63% to 100%. The Shannon diversity of the communities was 2.9 ± 0.2 bits/species (varied from 2.1 to 3.7 bits/species). The dominant species were *Phragmites australis* (Cav.) Trin. ex Steud. (projective cover 1–70%), *Ceratophyllum demersum* L. (1–50%), *Salvinia natans* (L.) All. (0–35%), *Typha latifolia* L. (0–35%), *Amorpha fruticosa* L. (seedlings) (0–15%), and *Hydrocharis morsus-ranae* L. (0–15%). The index of naturalness of this association was 2.9 ± 0.7 (in the range of 1.5 to 4.8). The index of hemeroby of this association was 44.0 ± 13.9% (in the range from 38.3% to 53.8%). The association prefers water with an electrical conductivity of 0.32 ± 0.12 dS/m (in the range of 0.08 to 1.30 dS/m), a temperature of 28.1 ± 1.5 °C (in the range of 25.2 to 30.2 °C), and an oxygen content of 12.1 ± 20.5 mg/L (in the range of 6.9 to 22.0 mg/L). The water transparency in the locations where this association occurs is 1.1 ± 0.1 m (in the range from 0.6 to 1.9 m). The phytoindication assessment of the light regime indicates a value of 7.0 ± 0.04 (in the range from 6.5 to 7.4). The temperature regime had a score of 4.8 ± 0.01 (in the range from 4.6 to 5.1). The continentality regime had a score of 8.8 ± 0.01 (in the range from 8.3 to 9.0). The humidity regime had a score of 8.1 ± 0.05 (in the range from 7.7 to 8.7). The acidity regime had a score of 6.9 ± 0.03 (in the range from 6.6 to 7.3). Nutrients' availability had a score of 6.8 ± 0.08 (in the range from 6.3 to 7.3).

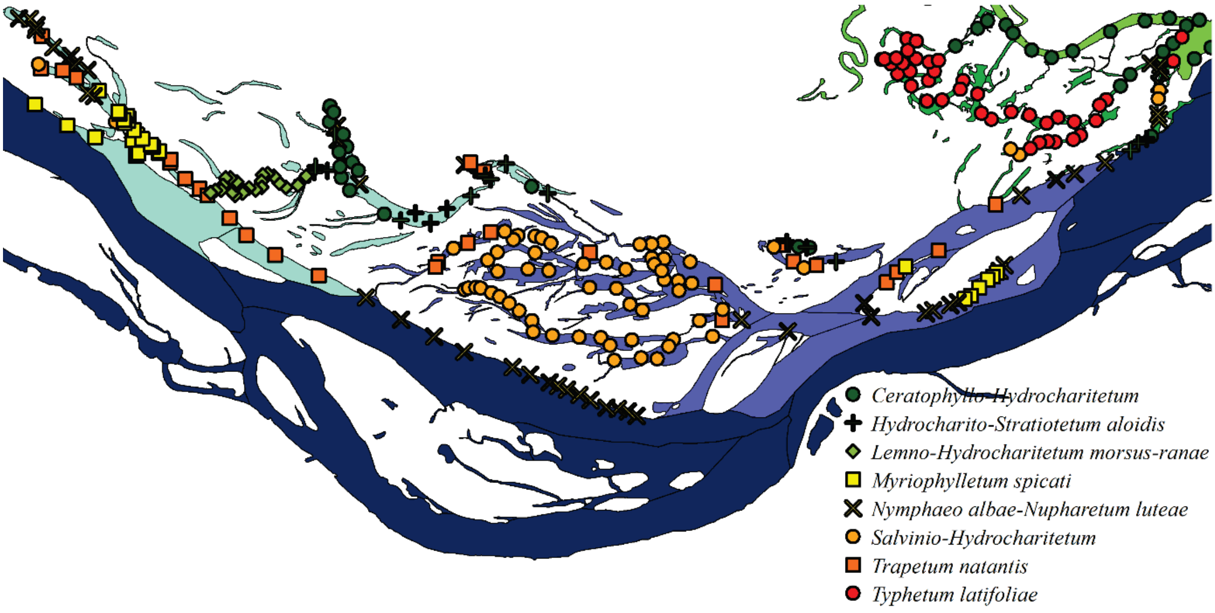

Fig. 1. Spatial distribution of aquatic vegetation associations within the reserve

The association *Lemno-Hydrocharitetum morsus-ranae* Oberd. 1957 included 21 plant species. On average, 16.1 ± 1.5 species were found on the survey plot (ranging from 15 to 20 species). The total projective cover varied from 56% to 100%. The Shannon diversity of the communities was 3.3 ± 0.1 bits/species (varied from 3.0 to 3.7 bits/species). The dominant species were *Salvinia natans* (L.) All. (projective cover 1–35%), *Nymphaea alba* L. (1–30%), *Typha latifolia* L. (1–35%), *Berula erecta* (Huds.) Coville (3–10%), *Spirodela polyrhiza* (L.) Schleid. (2–15%), and *Phragmites australis* (Cav.) Trin. ex Steud. (5–10%). The index of naturalness of this association was 5.2 ± 0.7 (in the range of 3.8 to 6.6). The index of hemeroby of this association was 35.1 ± 11.4% (in the range from 30.7% to 43.0%). The association prefers water with an electrical conductivity of 0.12 ± 0.01 dS/m (in the range of 0.08 to 0.23 dS/m), a temperature of 24.8 ± 1.2 °C (in the range of 23.5 to 28.2 °C), and an oxygen content of 8.1 ± 3.3 mg/L (in the range of 4.6 to 11.6 mg/L). The water transparency in the locations where this association occurs is 0.9 ± 0.1 m (in the range from 0.9 to 1.0 m). The phytoindication assessment of the light regime indicates a value of 7.2 ± 0.03 (in the range from 6.6 to 7.4). The temperature regime had a score of 4.8 ± 0.03 (in the range from 4.4 to 5.1). The continentality regime had a score of 8.5 ± 0.06 (in the range from 8.0 to 8.9). The humidity regime had a score of 8.3 ± 0.04 (in the range from 7.8 to 8.5). The acidity regime had a score of 6.7 ± 0.01 (in the range from 6.5 to 6.8). Nutrients availability had a score of 6.4 ± 0.03 (in the range from 6.1 to 6.9).

The association *Hydrocharito-Stratiotetum aloidis* (van Langendonck 1935) Westhoff in Westhoff et Den Held 1969 included 53 plant species. On average, 18.4 ± 8.7 species were found on the survey plot (ranging from 12 to 24 species). The total projective cover varied from 54% to 100%. The Shannon diversity of the communities was 3.4 ± 0.1 bits/species (varied from 2.8 to 4.0 bits/species). The dominant species were *Phragmites australis* (Cav.) Trin. ex Steud. (projective coverage 1–60%), *Nuphar lutea* (L.) Sm. (0–40%), *Ceratophyllum demersum* L. (5–35%), *Stratiotes aloides* L. (0–30%), *Typha latifolia* L. (0–35%), and *Spirodela polyrhiza* (L.) Schleid. (1–15%). The index of naturalness of this association was 3.8 ± 0.4 (in the range of 2.4 to 5.5). The index of hemeroby of this association was 46.3 ± 12.0% (in the range from 37.6% to 52.9%).

The association prefers water with an electrical conductivity of 0.12 ± 0.01 dS/m (in the range of 0.08 to 0.25 dS/m), a temperature of 27.3 ± 2.1 °C (in the range of 25.0 to 29.3 °C), and an oxygen content of 10.0 ± 7.8 mg/L (in the range of 3.6 to 18.8 mg/L). The water transparency in the locations where this association occurs was 1.0 ± 0.1 m (in the range from 0.7 to 1.7 m). The phytoindication assessment of the light regime indicated a value of 7.1 ± 0.03 (in the range from 6.6 to 7.4). The temperature regime had a score of 4.7 ± 0.02 (in the range from 4.5 to 5.0). The continentality regime had a score of 8.2 ± 0.18 (in the range from 7.5 to 8.8). The humidity regime had a score of 8.2 ± 0.04 (in the range from 7.7 to 8.5). The acidity regime had a score of 6.7 ± 0.01 (in the range from 6.5 to 6.9). Nutrients availability had a score of 6.7 ± 0.04 (in the range from 6.4 to 7.1).

Table 1

Synoptic phytosociological table (the table shows the percentage of species occurrences within the respective associations; the diagnostic species of the respective associations are marked in bold)

Species	Association*								φ	*P*-level
	As. 1	As. 2	As. 3	As. 4	As. 5	As. 6	As. 7	As. 8		
The number of *releve*	39	35	23	22	63	30	51	28		
Rumex hydrolapathum Huds.	**100**	51	100	64	70	7	31	11	0.84	<0.001
Carex pseudocyperus L.	**100**	51	100	36	60	27	4	7	0.82	<0.001
Mentha aquatica L.	**92**	9	–	18	65	13	4	14	0.79	<0.001
Typha latifolia L.	**95**	43	100	73	38	13	10	11	0.85	<0.001
Phragmites australis (Cav.) Trin. ex Steud.	**100**	100	100	100	95	93	88	39	0.96	<0.001
Bidens tripartita L.	**64**	54	–	41	40	10	20	14	0.66	<0.001
Sium latifolium L.	**21**	9	–	14	6	–	2	4	0.35	0.01
Ceratophyllum demersum L.	100	**100**	57	100	98	100	100	79	0.98	<0.001
Amorpha fruticosa L. (seedlings)	31	**77**	9	91	97	70	51	64	0.82	<0.001
Vallisneria spiralis L.	69	**63**	–	45	21	10	57	29	0.72	<0.001
Hydrocharis morsus-ranae L.	77	**94**	100	100	92	97	92	50	0.94	<0.001
Lemna trisulca L.	15	**14**	–	14	5	3	4	–	0.36	<0.001
Salix alba L. (seedlings)	–	6	**100**	9	5	–	4	–	0.8	<0.001
Lemna minor L.	18	71	**100**	82	70	70	47	32	0.81	<0.001
Nymphaea alba L.	41	37	**100**	59	63	27	27	36	0.71	<0.001
Carex acuta L.	15	29	**100**	32	27	17	–	61	0.8	<0.001
Lythrum salicaria L.	3	3	**91**	9	35	17	2	64	0.74	<0.001
Spirodela polyrhiza (L.) Schleid.	46	91	100	**100**	100	87	53	29	0.91	<0.001
Stratiotes aloides L.	10	43	100	**95**	87	73	82	39	0.89	<0.001
Salvinia natans (L.) All.	90	94	100	86	**100**	100	82	64	0.96	<0.001
Typha angustifolia L.	100	83	–	95	**98**	87	65	46	0.92	<0.001
Bidens cernua L.	36	40	100	82	**98**	67	18	32	0.88	<0.001
Lycopus europaeus L.	51	31	–	55	**92**	50	12	18	0.77	<0.001
Trapa borysthenica V.N. Vassil.	–	11	–	73	98	**100**	96	82	0.96	<0.001
Zizania latifolia (Griseb.) Stapf	8	–	–	5	60	**77**	67	79	0.82	<0.001
Nuphar lutea (L.) Sm.	–	54	–	91	40	90	**98**	82	0.91	<0.001
Cyperus flavescens L.	–	–	30	5	8	47	29	**100**	0.72	<0.001
Sparganium erectum L.	–	–	–	9	5	37	49	**89**	0.75	<0.001
Berula erecta (Huds.) Coville	82	71	100	68	100	87	22	**93**	0.93	<0.001
Cicuta virosa L.	92	66	9	41	97	57	4	**89**	0.89	<0.001
Najas marina L.	3	–	–	5	24	33	12	**89**	0.74	<0.001
Myriophyllum spicatum L.	–	6	–	14	13	47	59	**100**	0.92	<0.001
Caltha palustris L.	–	–	–	–	2	7	–	**32**	0.51	<0.001

Note: * – As. 1 are the diagnostic species of association *Typhetum latifoliae* Nowiński 1930, As. 2 are the diagnostic species of association *Ceratophyllo-Hydrocharitetum* Pop 1962, As. 3 are the diagnostic species of association *Lemno-Hydrocharitetum morsus-ranae* Oberd. 1957, As. 4 are the diagnostic species of association *Hydrocharito-Stratiotetum aloidis* (van Langendonck 1935) Westhoff in Westhoff et Den Held 1969, As. 5 are the diagnostic species of association *Salvinio-Hydrocharitetum* (Oberd. 1957) Boşcaiu 1966, As. 6 are the diagnostic species of association *Trapetum natantis* Kárpáti 1963, As. 7 are the diagnostic species of association *Nymphaeo albae-Nupharetum luteae* Nowiński 1927, As. 8 are the diagnostic species of association *Myriophylletum spicati* Soó 1927. Other species (numbers of associations where the species was found are in parentheses): *Epilobium hirsutum* L. (1, 4, 5), *Calystegia sepium* (L.) R. Br. (1, 2, 4), *Atriplex prostrata* Boucher ex DC. (1), *Bolboschoenus maritimus* (L.) Palla (2), *Scutellaria galericulata* L. (2), *Urtica dioica* L. (1, 2), *Thelypteris palustris* Schott (2, 3, 4), *Wolffia arrhiza* (L.) Horkel ex Wimm. (3), *Calamagrostis epigeios* (L.) Roth. (4), *Salix cinerea* L. (seedlings) (4), *Solanum dulcamara* L. (1, 4), *Galium palustre* L. (4), *Alnus glutinosa* (L.) Gaerth. (seedlings) (4), *Stachys palustris* L. (4, 7), *Spirogyra* sp. (2, 4, 7), *Frangula alnus* Mill. (seedlings) (2, 4, 7), *Carex riparia* Curtis (2, 4, 5, 6), *Epilobium roseum* Schreb. (2, 4, 5), *Epilobium tetragonum* L. (2, 4, 7), *Sagittaria sagittifolia* L. (2, 4, 5, 8), *Lysimachia thyrsiflora* L. (5), *Schoenoplectus lacustris* (L.) Palla (4, 5, 7, 8), *Butomus umbellatus* L. (5, 8), *Ceratophyllum platyacanthum* Cham. (4, 5, 6, 7, 8), *Persicaria minor* (Huds.) Opiz (5), *Pistia stratiotes* L. (6), *Agrostis stolonifera* L. (2, 7), *Aristolochia clematitis* L. (7), *Oenanthe aquatica* (L.) Poir. (7), *Salix caprea* L. (seedlings) (7), *Salix triandra* L. (seedlings) (7), *Rubus caesius* L. (7), *Populus alba* L. (seedlings) (7), *Glyceria maxima* (C. Hartm.) Holmb. (2, 4, 5, 7), *Typha laxmannii* Lepech. (8), *Cynodon dactylon* (L.) Pers. (6, 8), *Leersia oryzoides* (L.) Sw. (4, 6, 8), *Equisetum arvense* L. (8), *Lysimachia vulgaris* L. (1, 4, 5, 7, 8), *Plantago major* L. (8), *Rorippa palustris* (L.) Besser (8), *Persicaria hydropiper* (L.) Delarbre (2, 4, 5, 8), *Ranunculus repens* L. (5, 8), *Sparganium emersum* Rehmann (5, 8), *Digitaria ischaemum* (Schreb.) H.L. Muhl. (8).

The association *Salvinio-Hydrocharitetum* (Oberd. 1957) Boşcaiu 1966 included 47 plant species. On average, 19.7 ± 6.0 species were found on the survey plot (ranging from 15 to 28 species). The total projective cover varied from 67% to 100%. The Shannon diversity of the communities was 3.6 ± 0.1 bits/species (varied from 3.0 to 4.0 bits/species). The dominant species were *Phragmites australis* (Cav.) Trin. ex Steud. (projective coverage 0–40%), *Salvinia natans* (L.) All. (5–30%), *Typha angustifolia* L. (0–35%), *Trapa borysthenica* V. N. Vassil. (0–25%), *Stratiotes aloides* L. (0–30%), and *Bidens cernua* L. (0–25%). The index of naturalness of this association was 3.4 ± 0.4 (in the range of 2.2 to 4.8). The index of hemeroby of this association was 45.1 ± 25.6% (in the range from 30.4 to 54.8%). The association prefers water with an electrical conductivity of 0.15 ± 0.02 dS/m (in the range of 0.08 to 0.75 dS/m), a temperature of 25.1 ± 1.6 °C (in the range of 23.0 to 28.3 °C), and an oxygen content of 8.5 ± 9.8 mg/L (in the range of 3.6 to 16.5 mg/L). The water transparency in the locations where this association occurs was 0.7 ± 0.1 m (in the range from 0.3 to 1.1 m). The phytoindication assessment of the light regime indicated a value of 7.3 ± 0.02 (in the range from 6.9 to 7.5). The temperature regime had a score of 4.8 ± 0.02 (in the range from 4.5 to 5.1). The continentality regime had a score of 8.2 ± 0.15 (in the range from 7.3 to 8.8). The humidity regime had a score of 8.1 ± 0.02 (in the range from 7.8 to 8.4). The acidity regime had a score of 6.6 ± 0.01 (in the range from 6.5 to 6.8). Nutrients availability had a score of 6.8 ± 0.03 (in the range from 6.4 to 7.3).

The association *Trapetum natantis* Kárpáti 1963 included 36 plant species. On average, 16.3 ± 6.2 species were found on the survey plot (ranging from 12 to 21 species). The total projective cover varied from 62% to 100%. The Shannon diversity of the communities was 3.4 ± 0.1 bits/species (varied from 2.4 to 3.8 bits/species). The dominant species were *Trapa borysthenica* V. N. Vassil. (projective cover 1–30%), *Phrag-*

mites australis (Cav.) Trin. ex Steud. (0–35%), *Zizania latifolia* (Griseb.) Stapf (0–35%), *Salvinia natans* (L.) All. (1–20%), *Stratiotes aloides* L. (0–30%), and *Typha angustifolia* L. (0–30%). The index of naturalness of this association was 3.4 ± 0.6 (in the range of 1.5 to 4.7). The index of hemeroby of this association was 51.0 ± 18.1% (in the range from 43.7 to 57.5%). The association prefers water with an electrical conductivity of 0.12 ± 0.01 dS/m (in the range of 0.06 to 0.30 dS/m), a temperature of 26.3 ± 2.1 °C (in the range of 23.3 to 29.7 °C), and an oxygen content of 7.9 ± 5.8 mg/L (in the range of 3.2 to 24.3 mg/L). The water transparency in the locations where this association occurs was 0.9 ± 0.1 m (in the range from 0.5 to 1.2 m). The phytoindication assessment of the light regime indicated a value of 7.2 ± 0.02 (in the range from 6.9 to 7.5). The temperature regime had a score of 4.9 ± 0.02 (in the range from 4.6 to 5.1). The continentality regime had a score of 7.6 ± 0.27 (in the range from 6.6 to 8.5). The humidity regime had a score of 8.3 ± 0.03 (in the range from 7.9 to 8.5). The acidity regime had a score of 6.7 ± 0.02 (in the range from 6.4 to 7.0). Nutrients availability had a score of 6.8 ± 0.03 (in the range from 6.4 to 7.2).

The association *Nymphaeo albae-Nupharetum luteae* Nowiński 1927 included 46 plant species. On average, 13.4 ± 13.6 species were found on the survey plot (ranging from 7 to 25 species). The total projective cover varied from 48% to 100%. The Shannon diversity of the communities was 2.9 ± 0.2 bits/species (varied from 2.0 to 3.8 bits/species). The dominant species were *Ceratophyllum demersum* L. (projective coverage 1–50%), *Nuphar lutea* (L.) Sm. (0–40%), *Phragmites australis* (Cav.) Trin. ex Steud. (0–30%), *Zizania latifolia* (Griseb.) Stapf (0–35%), *Salvinia natans* (L.) All. (0–30%), and *Trapa borysthenica* V. N. Vassil. (0–20%). The index of naturalness of this association was 3.7 ± 0.6 (in the range of 2.1 to 5.6). The index of hemeroby of this association was 51.0 ± 25.3% (in the range from 29.7% to 57.9%). The association prefers water with an electrical conductivity of 0.12 ± 0.01 dS/m (in the range of 0.07 to 0.45 dS/m), a temperature of 28.0 ± 2.6 °C (in the range of 24.1 to 30.1 °C), and an oxygen content of 9.9 ± 8.5 mg/L (in the range of 3.0 to 21.9 mg/L). The water transparency in the locations where this association occurs was 1.0 ± 0.1 m (in the range from 0.6 to 1.4 m). The phytoindication assessment of the light regime indicated a value of 7.1 ± 0.05 (in the range from 6.6 to 7.6). The temperature regime had a score of 4.8 ± 0.03 (in the range from 4.5 to 5.2). The continentality regime had a score of 7.7 ± 0.32 (in the range from 6.2 to 8.9). The humidity regime had a score of 8.4 ± 0.05 (in the range from 8.0 to 8.9). The acidity regime had a score of 6.8 ± 0.03 (in the range from 6.5 to 7.2). Nutrients availability had a score of 6.9 ± 0.09 (in the range from 6.4 to 7.6).

The association *Myriophylletum spicati* Soó 1927 included 46 plant species. On average, 18.1 ± 22.7 species were found on the survey plot (ranging from 12 to 31 species). The total projective cover varied from 56% to 100%. The Shannon diversity of the communities was 3.2 ± 0.1 bits/species (varied from 2.5 to 3.9 bits/species). The dominant species were *Myriophyllum spicatum* L. (projective cover 3–50%), *Sparganium erectum* L. (0–30%), *Berula erecta* (Huds.) Coville (0–14%), *Cicuta virosa* L. (0–15%), *Carex acuta* L. (0–20%), and *Trapa borysthenica* V. N. Vassil. (0–10%). The index of naturalness of this association was 4.8 ± 0.6 (in the range of 3.2 to 6.1). The index of hemeroby of this association was 32.3 ± 39.3% (in the range from 24.3% to 51.9%). The association prefers water with an electrical conductivity of 0.09 ± 0.01 dS/m (in the range of 0.04 to 0.12 dS/m), a temperature of 23.7 ± 0.7 °C (in the range of 22.8 to 26.1 °C), and an oxygen content of 8.3 ± 8.1 mg/L (in the range of 2.0 to 18.5 mg/L). The water transparency in the locations where this association occurs was 1.0 ± 0.1 m (in the range from 0.8 to 1.3 m). The phytoindication assessment of the light regime indicated a value of 6.8 ± 0.04 (in the range from 6.5 to 7.3). The temperature regime had a score of 4.4 ± 0.02 (in the range from 4.3 to 4.9). The continentality regime had a score of 6.5 ± 0.26 (in the range from 5.1 to 7.1). The humidity regime had a score of 8.1 ± 0.04 (in the range from 7.8 to 8.5). The acidity regime had a score of 6.9 ± 0.02 (in the range from 6.7 to 7.3). Nutrients availability had a score of 6.3 ± 0.04 (in the range from 6.0 to 6.8).

The discriminant analysis extracted discriminant functions which can be meaningfully interpreted based on their correlation with variables representing environmental properties, Ellenberg indicator scales, and indicators of the level of anthropogenic transformation of the environment (Table 2).

Table 2
The correlations between the variables in the model and the discriminant functions

Variables		Discriminant function			
		Function 1	Function 2	Function 3	Function 4
Plant community properties	Species richness	–0.13	–	0.41	–0.20
	Shannon diversity, bit/species	–	0.19	0.54	–0.19
	Cover, %	0.18	–	–0.15	–0.19
Environment properties	Sand_Distance	0.21	–	–0.14	0.15
	EC, S/m	0.59	–0.52	–0.25	–0.26
	T, ºC	0.29	0.17	–0.58	0.30
	O_2 mg/L	0.12	–	–0.16	0.10
	Transparency, m	–	–	–0.31	0.45
Ellenberg indicators	Light Regime	0.13	0.37	0.35	–0.19
	Temp	0.20	0.34	–	0.13
	Continentality of climate	0.70	–	0.18	0.49
	Humidity	–0.16	0.24	–0.14	0.22
	Acidity	–	–0.30	–0.37	0.12
	Nutrients availability	0.24	0.32	–0.20	–0.18
Indicators of anthropogenic transformation	Naturalness	–0.29	–0.15	0.22	0.27
	Hemeroby	0.10	0.67	–0.38	–0.21

Function 1 correlates most strongly with the continental climate indicator and the electrical conductivity of water. This function clearly differentiates the *Myriophylletum spicati* associations, which are most common in the Dnipro riverbed, from *Typhetum latifoliae* associations, which are typical for the Obukhivka ledge system (Fig. 2). Function 2 results from the differentiation of plant communities along the hemeroby gradient. The highest hemeroby was observed in the *Nymphaeo albae-Nupharetum luteae*, *Hydrocharito-Stratiotetum aloidis*, *Salvinio-Hydrocharitetum*, and *Trapetum natantis* communities. This function indicates that the increase in hemeroby is also associated with an increase in light, temperature, and mineral nutrition, as well as a decrease in water salinity. Function 3 indicates the differentiating effects of water temperature and transparency, which also correlate with the light regime of plant communities. This function indicates that the Lemno-Hydrocharitetum morsus-ranae association prefers the lowest water temperature and transparency, but the highest light regime. The opposite preferences were demonstrated by the *Nympheo albae-Nupharetum luteae* association. These communities usually form under conditions of lower water salinity, higher water clarity, and warmer water. Function 4 is sensitive to the differential influence of water clarity and continental regime. The most transparent waters were preferred by the *Lemno-Hydrocharitetum morsus-ranae* communities, and the least transparent waters were preferred by the *Myriophylletum spicati*, *Typhetum latifoliae*, *Salvinio-Hydrocharitetum*, and *Trapetum natantis* communities.

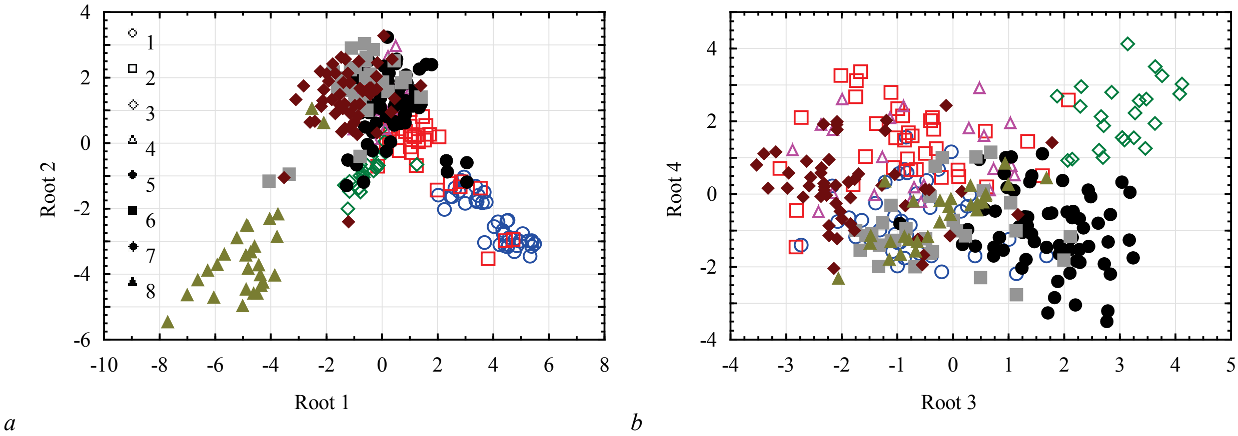

Fig. 2. The position of locations in the space of discriminant functions: *a* abscissa is Root 1, ordinate is Root 2, *b* abscissa is Root 3, ordinate is Root 4; associations: 1 is the association *Typhetum latifoliae* Nowiński 1930, 2 is the association *Ceratophyllo-Hydrocharitetum* Pop 1962, 3 is the association *Lemno-Hydrocharitetum morsus-ranae* Oberd. 1957, 4 is the association *Hydrocharito-Stratiotetum aloidis* (van Langendonck 1935) Westhoff in Westhoff et Den Held 1969, 5 is the association *Salvinio-Hydrocharitetum* (Oberd. 1957) Boşcaiu 1966, 6 is the association *Trapetum natantis* Kárpáti 1963, 7 is the association *Nymphaeo albae-Nupharetum luteae* Nowiński 1927, 8 is the association *Myriophylletum spicati* Soó 1927

Discussion

The recorded plant associations show a compact spatial distribution. The *Nymphaeo albae-Nupharetum luteae* Nowinski 1927 associations occur in the Dnipro riverbed. The *Ceratophyllo-Hydrocharitetum* Pop 1962 associations are typical of the Orilsky Canal water bodies and are also found in Sokilky Lake, which is part of the Mykolaivka ledge system. The communities of the association are common in the middle and lower reaches of the Dnipro River. They are widely distributed in non-flowing water bodies with weak water exchange, neutral or slightly alkaline reaction of the environment in wind-protected habitats, with water thickness up to 50 cm, silty bottom sediments with a significant detritus thickness and water transparency up to 15 cm. They are found in water bodies where excessive anthropogenic eutrophication processes are observed (Dubyna & Dzyuba, 2011). The association *Typhetum latifoliae* Nowinski 1930 occurs in the Obukhivka ledge system. The association *Salvinio-Hydrocharitetum* (Oberd. 1957) Boscaiu 1966 is mainly found in the water bodies of the Taromske ledge system. The association *Hydrocharito-Stratiotetum aloidis* (van Langendonck 1935) Westhoff in Westhoff et Den Held 1969 occurs in the water bodies of the Mykolaivka ledge system, which are close to the first floodplain terrace of the Dnipro River. The association *Lemno-Hydrocharitetum morsus-ranae* Oberd. 1957 is found in the channels of the Mykolaivka ledge system. The association Myriophylletum spicati Soo 1927 occurs in the bays of the Mykolaivka ledge system, which directly border the Dnipro riverbed. The association *Trapetum natantis* Karpati 1963 occurs in the water bodies of the Mykolaivka ledge system and the Taromske ledge system. The close spatial relationship of macrophyte associations with geomorphological areas of the Dnipro floodplain can help to reconstruct the events that led to the current appearance of plant communities. The morphology of reservoirs and their water properties were shown to largely determine the spatial distribution of aquatic macrophytes (Lukács et al., 2015).

The study found that the continental climate is an important differentiating factor that determines the characteristics of the vegetation cover of aquatic macrophytes. Climate continentality is a phytoindicative indicator that is derived from the characteristics of the range of the respective plant species. The continentality naturally varies from the oceanic climate in the west of the Eurasian continent to the ultracontinental climate in the east of Eurasia. Accordingly, species with a predominantly Western European distribution would indicate a preference for less continental conditions than species with an Eastern European distribution. Thus, the *Typhetum latifoliae* association differs from the others due to the dominance of plants with a range that is widespread in Eastern Europe. This association is found in the water bodies of the Obukhivka ledge system, where specific environmental conditions are formed. These include significantly higher water salinity, shallow water bodies that warm up well, and a relatively high supply of nutrients. It is also worth noting the low naturalness, which can be explained by the high level of bank erosion, which causes secondary succession of vegetation. The decrease in naturalness may be the result of increased secondary succession. A set of plants that share common habitat features can be interpreted as a flora. Thus, the communities of the Obukhivka ledge system are formed by flora of a different origin than the flora of the Dnipro riverbed and floodplain. The water bodies of the Obukhivka ledge system are the mouth of the steppe river Protich, the flora of which was most likely formed independently of the flora of the rest of the Dnipro floodplain. The most important feature of this flora is its greater continentality. The *Myriophylletum spicati* association is a collection of species that prefer a lower level of continentality, indicating the Eastern or Central European origin of the vast majority of plant species that form this association. This association tends to be located in the Dnipro riverbed. The floodplain associations occupy an intermediate position in terms of continentality compared to both *Typhetum latifoliae* and *Myriophylletum spicati* and actually form a third transitional group that is well distinguished from both of these associations. This gradient is characterised by a decrease in the number of species from the Dnipro riverbed to the Obukhivka ledge system and an increase in the projective cover of aquatic macrophytes. Thus, discriminant function 1 indicates the aspect of vegetation differentiation that is of natural origin.

Discriminant function 2 is a consequence of the impact of anthropogenic transformation of aquatic macrophyte communities, as evidenced by the important role of hemeroby in its determination. Hemeroby is combined with the availability of nutrients in water, which suggests that the eutrophication factor is the most important in the anthropogenic transformation of floodplain water bodies. The increased temperature is a factor in the development of eutrophication phenomena, which explains the positive correlation of the temperature indicator and water temperature with discriminant function 2. Hemeroby is also positively correlated with light regime and Shannon's diversity, while there is no correlation with the number of species. This indicates that an increase in hemeroby is accompanied by an equalisation of the projective cover of different species. The highest level of hemeroby was found for four associations. It should be noted that the associations associated with the Dnipro riverbed are characterised by both the highest (*Nymphaeo albae-Nupharetum luteae*) and lowest (*Myriophylletum spicati*) levels of hemeroby. The high level of hemeroby in the Dnipro riverbed can be explained by both the high level of bank erosion and the level of pollution of the Dnipro water. The *Myriophylletum spicati* community is associated with high sandy banks, which can be a source of condensation moisture that can dilute the toxic waters of the Dnipro River. This assumption is supported by the fact that the electrical conductivity of the water where *Myriophylletum spicati* associations occur is the lowest of all the measurements made. Thus, discriminant function 2 can be meaningfully interpreted as eutrophication of water bodies induced by nutrient content.

Discriminant function 3 indicates the importance of the temperature gradient in differentiating plant communities. Temperature affects the level of oxygen consumption in water by living organisms and decaying organic matter. It can significantly influence the manifestation of eutrophication phenomena, which also explains the correlation of this function with the hemerobia indicator. Thus, discriminant function 3 can be meaningfully interpreted as the level of intensification of eutrophication phenomena that occur as a result of temperature increase. Obviously, the temperature increase is sharp at the end, because plant communities do not have time to react by changing their structure, because the temperature indicator did not correlate with discriminant function 3. An increase in temperature promotes macrophyte overgrowth in water bodies, as evidenced by the correlation of discriminant function 3 with projective cover. The increase in projective cover induced by higher temperature is accompanied by a decrease in the number of species in the community and species diversity. This is a typical pattern of stimulating the growth of certain plant species during eutrophication.

The transparency gradient correlating with continentality is represented by discriminant function 4. The *Lemno-Hydrocharitetum morsus-ranae* association prefers the most transparent waters. These associations are compactly located in the channels of the Mykolaivka ledge system. The diversity of such communities is somewhat lower, indicating the presence of certain environmental filters that allow plants to exist in conditions of high water flow. The high role of the continentality marker indicates the habitat similarity of the plant species that make up this association, which could have arisen under conditions of their long-term coevolution. It should be noted that the *Lemno-Hydrocharitetum morsus-ranae* association is usually more natural and less hemerobic.

Conclusion

The vegetation cover of macrophyte communities in the Dnipro-Orel Nature Reserve is represented by eight associations. Their differentiation is due to natural factors and factors caused by anthropogenic impact. The high level of naturalness of the communities indicates the role of the conservation regime in the conservation of biological diversity. However, the protection regime alone cannot shield the reserve from the effects of a complex of anthropogenic factors. The continental gradient is the most important for differentiating the vegetation cover of floodplain ecosystems. It divides the vegetation cover into three homogeneous zones: the Dnipro riverbed, the Obukhivka ledge system and other floodplain reservoirs. The main feature of the ecological conditions of the Obukhivka ledge system is the high level of salinity, relatively shallow depth of the water bodies and their ability to warm up very quickly. Water in the Dnipro riverbed has the lowest level of salinity. The anthropogenic transformation of plant communities is caused by eutrophication, which depends on both the presence of excessive amounts of nutrients and water temperature. The refugia of rheophilic regimes in the Dnipro River floodplain form centres of biodiversity that have high naturalness and significant environmental value. Indicators of naturalness and hemeroby are sensitive markers of the state of plant communities that can be used in the practice of biological monitoring in nature reserves.

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