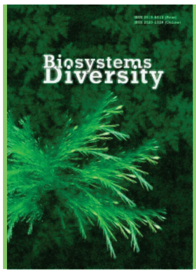

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Morphological and functional diversity of floodplain water bodies and their classification according to the structure of the surrounding vegetation cover

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The study identified the indicators of functional and morphological diversity of the Dnipro River floodplain water bodies within the Dnipro-Orilsky Nature Reserve. The database of recorded water bodies of the reserve consists of 302 objects. The total area of the floodplain and the water bodies close to it is 24.2 km^2, and the area of the water bodies is 6.03 km^2. Thus, the water bodies cover 24.9% of the floodplain area. The water bodies of the Dnipro River channel system account for 17.9% of the number of water bodies in the Reserve and 71.4% of the total area of water bodies and the Dnipro River in the projection of the Reserve. The water bodies of the study system are located at a distance of up to 3.2 km from the main channel of the Dnipro River. The average distance is 1.50 ± 0.04 km. The closest water bodies to the main channel of the Dnipro River are those in the Dnipro riverbed, which were formed as a result of the creation of a reservoir in the floodplain. Three factors with eigenvalues greater than unity were extracted as a result of factor analysis of the morphometric features of the water bodies. These three factors explain 85.8% of the cumulative correlation of morphometric features. Factor 1 reflects a latent variable that can be identified as the total size of the ponds. The total size of the water bodies was the largest for the Orilsky Canal, with slightly smaller sizes in the water bodies of the Dnipro River channel. The smallest water bodies were in the Obukhivka system. Factor 2 as a latent variable can be identified as the level of shoreline development. According to this indicator, the water bodies of different systems did not differ. Factor 3 can be identified as the altitude and variability of the relief surrounding the water bodies. The lowest values of this factor were for the water bodies of the Orilsky Canal and the Obukhivka system. The values were slightly higher for the water bodies of the Taromske and Mykolaivka systems. The highest levels of relief and its variability were characteristic of the areas close to the water bodies of the Dnipro channel system. Cluster analysis allowed us to identify seven clusters that are relatively homogeneous in terms of morphometric features. These clusters can be differentiated based on the results of discriminant analysis. An important aspect of differentiation is the size of the water bodies, the development of the shoreline, and the height of the terrain surrounding the water bodies. The identified clusters correspond well to the types of water bodies, which are selected based on their orientation relative to the preferred direction of water flow. The satellite image classification was used to identify 15 types of vegetation cover within the reserve. The water bodies are characterized by specific spectra of the main types of plant communities in their surroundings. The cluster analysis of the water bodies resulted in nine clusters based on the structure of the vegetation complexes surrounding them. Each cluster contains the entire list of vegetation types that have been established for floodplain ecosystems. The peculiarity of the complexes lies in the specific ratio between different vegetation types. The most important structural factors that distinguish the complexes are the projective cover of oaks, floodplain meadows, and shrubs. At the top level of the hierarchy, the complexes are differentiated by the projective cover of floodplain meadows. At a lower level, the differentiation is based on the projective cover of sands or oaks. The clusters identified on the basis of plant complexes and morphometric features, as well as the types of water bodies in terms of orientation with respect to the prevailing water flows, correspond to each other to a certain extent.

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

Introduction

The European Water Framework Directive (2000/60/EC) is the most comprehensive EU strategy in the water sector in decades. All EU member states and candidate countries have to adapt their water management systems to the objectives of the Water Framework Directive and implement integrated river basin management, which involves diverse research (Mostert, 2003). The Water Framework Directive requires a number of analyses and extensive monitoring, as well as a study of the features of different river basin areas to provide the proposed river basin management system. The development of a typology of water bodies and the definition of environmental reference conditions for each type is recognized as important (Zymaroieva et al., 2022). They will serve as a basis for determining the "good ecological status" to be achieved as a result of management. The key areas of typology are geography and geology (size, shape, location, etc.), biological quality elements (phytoplankton, fish fauna, etc.), hydromorphological quality elements (hydrological regime, river continuity, etc.), and chemical and physico-chemical quality elements (thermal conditions, salinity, specific pollutants, etc.) (Wallin, M., Wiederholm, T., & Johnson, R. 2003. Guidance on establishing reference conditions and ecological status class boundaries for inland surface waters (7.0 final). CIS Working Group 2.3). Floodplain lakes include all continental water bodies with a basin formed as a result of fluvial processes, and their limnological functioning is determined by irregular but periodic limnophases and potamophases (Dawidek & Ferencz, 2012). A lake is considered to be classified as a floodplain lake if it is located on a floodplain and has some obvious connection to a main stream, is located within fifteen stream widths of the main stream, contains water including at least one sickleshaped section (the so-called "fundamental component"), is of the same order of size as the main stream and is independent of other topographic influences, i.e. each floodplain lake must be separate from the others (Weihaupt, 1977). Floodplain lakes can represent either lentic or lotic environments, or a combination of both in different parts of the lake basin (Ferencz et al., 2023). Dynamic geomorphological processes occur in the river valley and especially in its floodplain, depending on the geological structure, topography, morphology and type of river, climatic conditions and vegetation cover (Tsvetkova & Saranenko, 2007, 2010; Saranenko, 2011; Tsvetkova et al., 2015; Wierzbicki et al., 2020). Natural river lakes can be divided into lakes in the river valley and channel lakes (Dawidek & Ferencz, 2012). Artificial reservoirs are a distinct group of water bodies that cannot be classified as lakes due to their anthropogenic origin (Havlíček et al., 2022). These reservoirs are, however, located in river valleys, and human activities in terms of water distribution, flushing times and water circulation play a significant role in the physical, chemical and biological functioning of the reservoirs (Akhtar et al., 2021).

The periodic occurrence of the potamophase and limnophase is the key feature of floodplain lakes (Bondarev et al., 2022). The course of these phases affects the productivity and diversity of the biota of reservoirs (Napiórkowski & Napiórkowska, 2017). The timing, range, and intensity of potamophases and limnophases determine the functioning and environmental integrity of the adjacent floodplain (Ferencz et al., 2023). The hydrologic regime of floodplain lakes is the result of four cyclic phases: filling, inundation, drainage, and isolation (García de Emiliani, 1997). Other studies distinguish two phases: flooding or potamophase and isolation or limnophase (Schemel et al., 2004). During the limnophase, intralake processes determine the characteristics of the lake (Napiórkowski & Napiórkowska, 2017). Relatively stable limnophase conditions favor the growth of macrophytes and many algae groups (Reckendorfer et al., 2013). The lake is supplied from the catchment area, and this shapes the type and intensity of hydrochemical and hydrological processes. Periods of limnophase stability are usually interrupted by periods of flooding with great regularity (Chaparro et al., 2016). The inflow of water from the river raises the water level in the floodplain lakes (Riis & Biggs, 2003). Living organisms are washed away, and the sediments accumulated during the limnophase are washed out (Kunakh et al., 2022). Water transparency decreases dramatically as river water carries a huge amount of suspended solids (Zymaroieva et al., 2022). This negatively affects macrophytes, which die due to lack of sunlight. Over time, small organisms brought by the river, such as diatoms and rotifers, begin to dominate (Dembowska, 2015). During the potamophase, there is a significant correlation between the physicochemical parameters of the lake and its basin. The duration of the potamophase determines the water quality of the floodplain lake, expressed by the hydrochemical type (Ferencz et al., 2020). At potamophase, the catchment area expands and is equal to the catchment area of the river up to the channel that feeds the lake basin. Floodplain lakes can completely lose their identity during floods, turning into a hollow in the floodplain. The natural physical processes that determine the functioning of floodplain lakes depend on the duration and intensity of the potamophase and limnophase. Based on the duration of the phases, the Fluvial Connectivity Quotient (FCQ) can be calculated, which is the ratio of the number of days of flood duration to the number of days during which the lake is in an isolated state (Poi de Neiff et al., 2006).

The fluviodynamic and hydraulic capacity of a river determines the processes of accumulation or erosion of mineral substances in lake basins (Szmańda et al., 2021), and are also the main factors that shape the thermal, optical and oxygen regimes of water (Rajwa-Kuligiewicz et al., 2015). The origin of a lake is associated with fluvial processes that determine the distribution of water and its quantity in the basin (Paira & Drago, 2007). The vast majority of floodplain lakes become running water in the course of the potamophase and due to the excessive supply of water in the form of river runoff, precipitation and surface runoff, the bathymetric characteristics of floodplain lakes change rapidly (Lesack & Melack, 1995). There is a variety of water circulation regimes in floodplain lakes (Na & Li, 2022). Lakes can be hydraulically connected to the river in the upper reaches, which facilitates the flushing of lake water, or in the lower reaches, through a fissure. Such a connection in the downstream area results in a longer period of lake isolation and maintains specific physicochemical parameters of the lake water. This type of feeding contributes to the physicochemical autonomy of lake waters. The highest level of supply is usually observed in the vicinity of the gorge due to underground infiltration from the surrounding hydrogeological unit (Dawidek & Ferencz, 2012). The hydrochemical and hydrobiological qualities of lake water are determined by the direction and intensity of lake influx (Vasistha & Ganguly, 2020). Aquatic biota habitat conditions depend on the dynamics and regimes of water turnover in lakes. The conception of the flood pulse is the basis for understanding the ecological functioning and biodiversity of floodplain lakes. The degree to which lake ecosystems are affected by water level fluctuations strongly depends on the morphology of the lake. Shallow lakes or lakes with large shallow margins are shown to be the most sensitive to the effects of water level changes (Wantzen et al., 2008).

The simplest classifications of floodplain lakes are derived from the shape and development of the shoreline. Three types of lakes were recognised based on the morphometry of oxbows. The first classification was based on the degree of complexity and included three categories: simple oxbows, compound oxbows and complex oxbows. The second classification was related to the level of closure of the oxbow limbs and also consisted of three categories: open oxbows, normal oxbows and closed oxbows (Weihaupt, 1977). The shape of the floodplain lake basin allows one to trace their origin. The lake basins were classified into the following main forms: round-oval, elongated and irregular. Circular-oval lakes include round, elliptical and "drop" shape basins (Paira & Drago, 2007). A large number of round-oval lakes are usually located on older floodplain areas. Many younger round-elliptical and drop-shaped lakes are also formed on the islands of the main channel of floodplain areas (Hutchinson, 1957). Old round lakes are usually associated with wetlands and have shores with very gentle slopes covered with aquatic and marsh vegetation. They are isolated from running water for a long time. Island lakes, on the other hand, are located on channel islands and are completely surrounded by berms, so their isolation phases are short. Elongated lakes are lakes with channel-like depressions that have "wide" and "thin" hollows. They are well-defined channel-like depressions formed by the abandonment of meandering main river channels or sections of floodplain channels. Meander loops (wide hollows) and other abandoned straight and meandering secondary channels retain their channel form over long periods of morphological evolution, mainly in wide channels with greater depths. There are many lakes formed in oxbows that did not arise as a result of the abandonment of a single meander. Such channels are meandering or former meandering channels abandoned by siltation and cutting of new channels and are common within the anastomosing complex. Some of these genetically shallow lakes are subject to sedimentation in the same way as small oxbows, but they are less sinuous and often eroded during floods when their main axis is parallel to active secondary channels. In contrast, very shallow meandering lakes lose their channel shape more quickly due to their shallow depths and also due to the confluence of several meandering depressions that usually belong to the same meandering set of meandering lakes (Paira & Drago, 2007).

Floodplain lakes typically exhibit significant chemical and ecological differences, even though they are usually filled from a common source of river water (Forsberg et al., 1988). A significant number of differences between the conditions of biota habitat in lakes are due to the morphological features of lake basins (Melack, 1984). For example, the morphometric features such as lake volume, mean depth, shallowing rate and volume change were the parameters that correlated most strongly with the proportion of macrophytes in lakes (Lawniczak-Malińska et al., 2018). Lake basin morphology and hydrology determine the dynamics of algal blooms in highly eutrophic shallow lakes. Water quality is better in lakes that are hydraulically connected to rivers compared to those that are isolated from the river (Huang et al., 2014). The ecological status of lakes connected to rivers is the best, as evidenced by high levels of biodiversity, biomass and macroinvertebrate production (Pan et al., 2014). Floodplain lakes can be classified according to the main direction of water circulation (van der Steeg et al., 2023). Vertical water exchange drives evaporation-dominated lakes, while horizontal exchange drives flood-dominated lakes (Kuriata-Potasznik et al., 2020). The ratio of length to width of the water body is considered to be the main factor in the classification of floodplain lakes during the limnophase. The morphometric classification of lakes also indicates their biological characteristics. Lake fish communities were found to be predominantly dependent on lake area, length (length to width ratio) and, to a lesser extent, water clarity (Miranda & Lucas, 2004). Based on the value of this ratio, two types of lakes were distinguished: channel lakes with a short retention time, where this ratio exceeded 5, and plate lakes with a longer retention time and a ratio value of less than 5 (Hamilton & Lewis, 1990). More than 90% of rivers in Europe and North America were estimated to have been altered by anthropogenic impacts (Wolf et al., 2021). The human pressure on river valleys changed the duration, frequency and intensity of natural floods (Angelakis et al., 2023), affecting the balance of the natural functional regimes of floodplain ecosystems such as the potamophase and limnophase (Ferencz et al., 2023).

The vegetation in floodplains has an impact on the water level in lakes, as well as the flow rate and water discharge in rivers. The construction of a dam can cause changes in the flow regime, which in turn can accelerate changes in the structure of the vegetation cover of river floodplains (Huang et al., 2023). The interaction between vegetation and hydrology varies depending on the seasonality of floodplains. Floodplain vegetation emergence reduces flow velocity and raises water levels, affecting the efficiency of water transportation in the system. The structure of floodplain vegetation is closely related to the distribution of flow velocity (Li et al., 2020). The vegetation found in the floodplain is influenced by various factors such as the morphology and age of the lakes, livestock access to the shoreline, flood duration, and the area of lake sediments exposed at low water levels (Van Geest et al., 2005). Vegetation can reduce the active width of a watercourse and alter the velocity of water flow on hydrometric verticals within the floodplain and main channel. It is important to note that this effect is not always negative and can have both positive and negative impacts on the ecosystem (Walczak et al., 2018). The flood regime, in turn, affects the structure of the floodplain vegetation (Wu et al., 2022). Macrophyte species richness is affected by water level fluctuations (Geest et al., 2005). Thus, vegetation cover and floodplain water bodies are closely related, but the problem of the possibility of using the features of the canopy cover to classify floodplain water bodies has not been practically solved.

The aim of this study was to identify indicators of functional and morphological diversity of the Dnipro River floodplain water bodies within the Dnipro-Orilsky Nature Reserve and to assess the importance of vegetation cover in the surrounding area for understanding the genesis and dynamics of floodplains.

Material and methods

The research was conducted in the summer of 2023 within the waters of the Dnipro-Orilsky Nature Reserve (Dnipro region, Ukraine). The water bodies of the reserve are divided into the following systems: water bodies of the Dnipro riverbed, those of the Orilsky Canal (an artificial formation), water bodies of the Mykolaivka ledge system, Obshivka ledge system, and the Taromske ledge system (Fig. 1). The current area of the Reserve is considered with the projected areas that can be added to the territory of the Reserve due to their high conservation value. The water bodies were surveyed, during which their depths were measured using a Humminbird HELIX 9 CHIRP MEGA SI+ GPS G4N echo sounder. The area of the studied water bodies was relatively evenly covered with measurement points. The coordinates of the measurement points were recorded using a GPS device. The configuration of the water bodies was recreated using detailed satellite images from the Bing Maps service (www.bing.com/maps), and was also refined during field research. The depth map of the Dnipro River channel was based on the Navionics SonarChart data™ (www.navionics.com). The data from the Advanced Land Observation Satellite – ALOS (www.eorc.jaxa.jp/ALOS/en/index.htm) were used to create the digital elevation model. The spatial resolution for this model is 12.5 meters. The DEM was resampled to a resolution of 1 m using the kriging procedure (Susetyo, 2016). The digital elevation model was merged with the digital bottom model to create an integrated digital elevation model of the surface and underwater terrain. The morphometric characteristics of the water bodies were calculated using the lakemorpho (Hollister & Stachelek, 2017). The list of morphometric characteristics of water bodies is given below.

Lakes' morphometric parameters. Shoreline length and surface area. The length of the shoreline is clearly the overall perimeter of the polygon of the lake. Analogously, the surface area of a lake is the total area of the polygon of the lake (Hollister & Stachelek, 2017). The surface area and length of the shoreline of water bodies are significant drivers of waterbird density (Pescador et al., 2012) and macrophyte community structure (Grzybowski et al., 2022).

Shoreline development. The shoreline development metric assesses the degree of complexity of the shoreline. It is the ratio of the perimeter of a body of water to the perimeter of a circle of the same area. The value will be 1 or greater, with a value of 1 indicating a circular body of water. The shoreline development index is a good indicator of habitat potential (Kaufmann et al., 2014) and is a basic metric of lake morphometry (Wetzel, 2001), widely used to describe the planar shape of lakes in hydrographic studies (Messager et al., 2016), and is used as an explanatory predictor in statistical analyses (Casas-Ruiz et al., 2021).

Maximum depth. The maximum depth of a lake provides information that can be used in conjunction with flow velocity to estimate the time a lake exists. A variety of ecosystem regimes, such as mixing and thermal stratification (Lewis, 1983), the relative extent of littoral and pelagic habitats (Seekell et al., 2021), and carbon cycling, including methane evasion (Li et al., 2020), depend on the maximum lake depth.

Mean depth. Mean depth of a lake is calculated as the volume of the lake divided by the area. Mean lake depth affects the productivity of fish communities (Rawson, 1952). Lake depth, along with lake surface area, water clarity and dissolved oxygen levels, are the most important factors in structuring lake fish communities (Lubinski et al., 2008).

Volume. The lake volume function uses maximum lake depth and to estimate lake volume (Hollister & Milstead 2010). The method assumes that the maximum in-lake distance (Dmax) from the shoreline is also the deepest part of the lake (Zmax). The lakeVolume function creates a raster of the in-lake distance to shoreline and converts those distances, using Zmax:Dmax, to depths and then summing the volume of each pixel to estimate total lake volume.

Maximum length. Maximum lake length is the longest stretch of open water across a lake and, like fetch, is a measure of mixing potential (Wetzel, 2001).

Maximum and mean width. Maximum lake width is the largest distance from shore to shore orthogonal to the line indicating the greatest lake length, and is also a measure of mixing (Wetzel, 2001). The mean width of a lake is calculated as lake area divided by maximum lake length.

Major and minor axis. The major axis of a lake is considered to be the longest line intersecting the convex hull surrounding the polygon and crossing through its centre. It represents the distance across the lake, without taking into account the land and water configuration, in contrast to the maximum length of the lake. The minor axis of a lake is defined as the shortest line intersecting the convex hull formed around the lake polygon while passing through its center. In contrast to lake maximum width, its value represents the distance across a lake with regard to the convex hull and without consideration of the land-water configuration.

Axis ratio. The ratio of the length of the major axis of the lake to the length of the minor axis is also known as the aspect ratio. A circular body of water has an aspect ratio that approaches 1, while an elongated body of water has an aspect ratio that approaches 0.

Fetch. The fetch is the maximum distance to open water in a given direction, which is an indicator of water mixing in a water body, as a larger fetch means a greater potential for waves due to wind (Scheffer, 2004). The inorganic sediment particles as well as algal cells undergo a rapid cycle of sedimentation and resuspension in many shallow lakes. The resuspension is often driven primarily by waves, but in some situations, fish searching for food on the bottom can also stir up significant amounts of sediment. Information about the distance that the wind carries over the water (the "fetch"), as well as wind speed and water depth, can predict the intensity of resuspension (Bengtsson & Hellström, 1992).

Hydrological classification of floodplain lakes. The direction of the water flow can also be a criterion for the hydrological classification of floodplain lakes (Dawidek & Ferencz, 2005). The water bodies were classified into contrafluent, confluent, contrafluent-confluent, bays and river channels according to the direction of the preferential water flow (Fig. 1b).

If the direction of inflow and the inclination of the valley coincide, as in the case of an upstream connection, floodplain lakes with high water exchange dynamics are formed, which are classified as confluent floodplain lakes. In contrast, lakes with an active gorge are supplied downstream and upstream, and are classified as contrafluent floodplain lakes.

There may also be a mixed supply of water to the lake. Such lakes are referred to as contrafluent-confluent floodplain lakes. Also, a significant amount of water in the lake may remain without water exchange, in which case such lakes are classified as profundal floodplain lakes (Dawidek & Ferencz, 2012). When the lake is supplied through two channels, the autochthonous water is directed towards the centre of the basin, forming a contrafluent-confluent floodplain lake. There are also tributary or counterfluid lakes that are fed by groundwater. If the groundwater flow is powerful enough to determine the water level at the limnophase stage, the lake is called a deepwater lake. Intra-lake processes are shaped by hydrophysical factors, as well as the hydrochemistry of the floodplain lake catchment and the hydrobiology of its basin. The quality of lake water depends on the location of the lake in the river valley and the availability of river water, which is reflected in the lake's eutrophication. There are three types of lakes, and within each of them three more types can be distinguished based on catchment conditions and water quality (Dawidek & Ferencz, 2005).

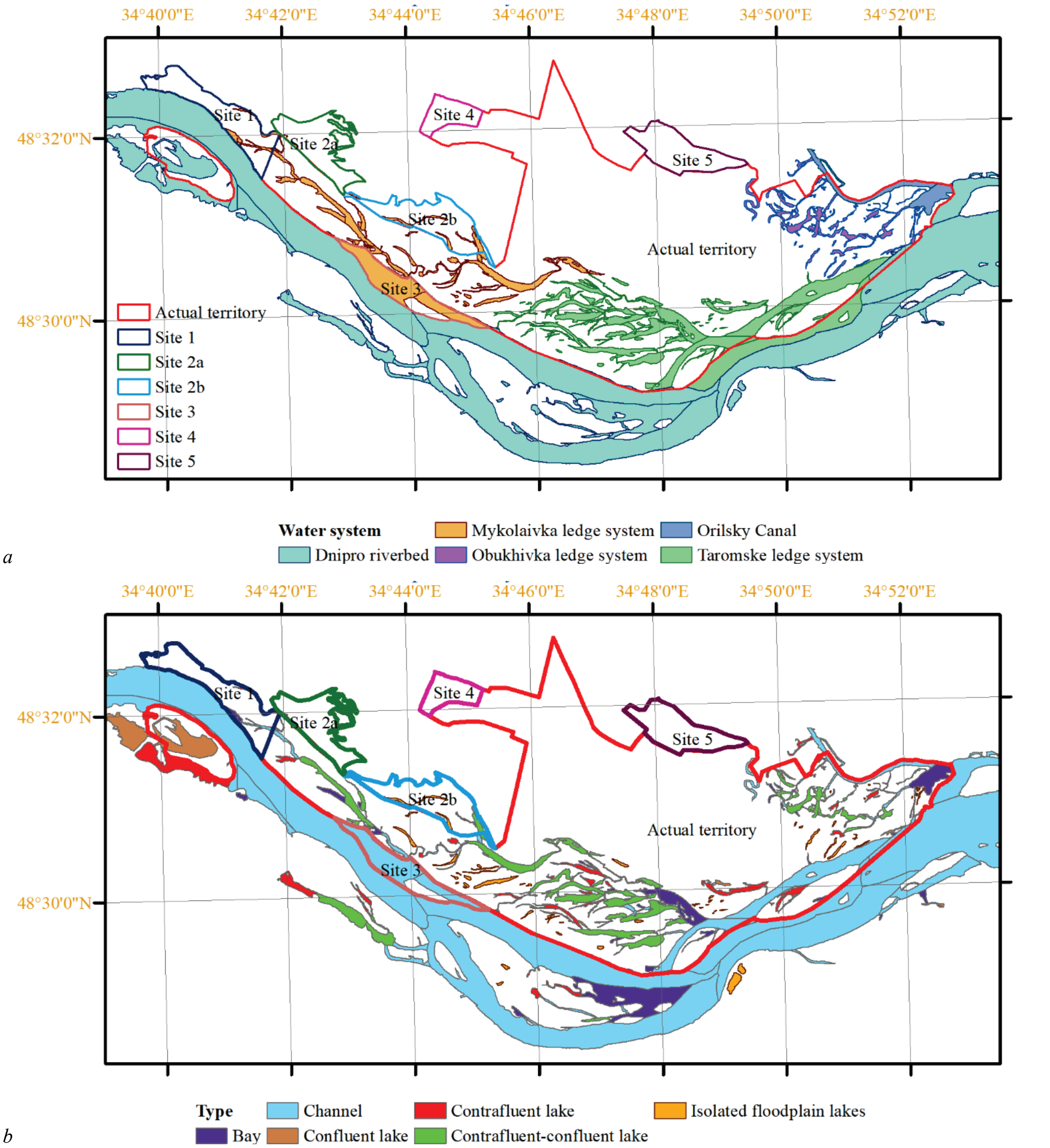

Fig. 1. Systems of water bodies within the nature reserve: *a* – the red line shows the boundary of the reserve; sites 1–5 are the territories that are planned to be included in the reserve; *b* – classification of the reserve's water bodies according to their orientation to the prevailing direction of water flow

The classification of vegetation types was based on Sentinel-2 satellite image (https://dataspace.copernicus.eu), which was acquired on June 20, 2023. All layers were converted to a resolution of 10 meters using the SNAP Desktop program (https://step.esa.int/main/download/snap-download). The classification was performed in ArcGIS 10.0. The resulting clusters were decoded based on field research. The descriptive statistics were calculated, as well as cluster, factor, discriminant, and ANOVA analyses, using the software Statistica 10.0 (Statsoft, USA).

Results

Morphometric traits of water bodies depending on the water system. The database of recorded water bodies in the Reserve includes 302 objects. The total area of the floodplain and the reservoirs close to it is 24.2 km^2, and the area of the water bodies is 6.03 km^2. Thus, the water bodies cover 24.9% of the floodplain area. The water bodies of the Dnipro River channel system account for 17.9% of the number of ponds in the Reserve and 71.4% of the total area of ponds and the Dnipro River in the projection of the Reserve. The water bodies of the Mykolaivka ledge system account for 20.2% of the total number and 8.2% of the total area of water bodies. The water bodies of the Obukhivka ledge system account for 29.1% of the total number and 2.9% of the total area of water bodies. Water bodies of the Orilsky Canal account for 0.7% of the total number and 2.0% of the total area. The water bodies of the Taromske ledge system account for 32.1% of the total number of water bodies and 15.4% of the total area of water bodies in the Reserve. The water bodies of the study system are located at a distance of up to 3.2 km from the main channel of the Dnipro River. The average distance is 1.50 ± 0.04 km. The closest water bodies to the main channel of the Dnipro River are those of the Dnipro riverbed, which were formed as a result of the creation of a reservoir in the floodplain. The closest water bodies to the Dnipro River are those of the Mykolaivka ledge system (Planned comparison F = 12.3, P < 0.001, Table 1). The distance to the Dnipro riverbed of the water bodies of other systems is not statistically significantly different (planned comparison F = 0.004, P = 0.95). The lowest level of relief surrounding the water body was in the Obukhivka ledge system, and the highest in the Dnipro riverbed system. The water bodies of the Taromske and Mykolaivka ledge systems did not differ from each other by this parameter (planned comparison F = 0.81, P = 0.37). The variability of relief altitude was statistically significantly correlated with relief altitude (R = 0.37, P < 0.001). Therefore, this indicator repeated the pattern of relief altitude. The largest water bodies in terms of surface area were those in the Dnipro River channel system and the Orilsky Canal. Other water bodies did not differ in this indicator (planned comparison F = 0.37, P = 0.55). The mean depth was greatest in the Orilsky Canal. This indicator was somewhat lower in the water bodies of the Dnipro River channel. The water bodies of the Taromke and Mykolaivka ledge systems did not differ in this indicator (planned comparison F = 0.04, P = 0.85). The mean depth of water bodies in the Obukhivka ledge system was the smallest (planned comparison F = 3.2, P = 0.05). The level of shoreline development within the water systems did not differ statistically significantly. The axis ratio was the highest for the Orilsky Canal water bodies, with a slightly lower value for the Obukhivka ledge system and the Dnipro riverbed system. The lowest axis ratio was for the water bodies of the Mykolaivka and Taromske ledge systems.

Table 1
Descriptive statistics of morphometric characteristics of water bodies depending on the water system

Variable	Dnipro riverbed, N = 54	Mykolaivka ledge system, N = 61	Obukhivka ledge system, N = 88	Orilsky Canal, N = 2	Taromske ledge system, N = 97	R^2	*P*-level
Distance to Dnipro stream bed, km	0.6 ± 0.1	1.2 ± 0.1	1.9 ± 0.1	1.7 ± 0.5	1.8 ± 0.1	0.49	<0.001
Mean relief altitude within the buffer, m	56.0 ± 0.3	54.1 ± 0.3	51.9 ± 0.2	52.8 ± 0.3	54.1 ± 0.2	0.40	<0.001
SD relief altitude within the buffer	2.6 ± 0.1	2.2 ± 0.1	1.8 ± 0.1	2.8 ± 0.1	2.0 ± 0.1	0.16	<0.001
Surface area, ha	35.6 ± 12.0	3.6 ± 1.3	0.9 ± 0.1	27.1 ± 2.8	4.3 ± 1.4	0.19	<0.001
Shoreline length, km	3.0 ± 0.6	1.1 ± 0.2	0.6 ± 0.1	5.7 ± 2.9	1.1 ± 0.2	0.15	<0.001
Shoreline development	2.2 ± 0.1	2.3 ± 0.1	2.1 ± 0.1	3.0 ± 1.4	2.3 ± 0.1	0.01	0.59
Max depth, m	4.5 ± 0.7	1.5 ± 0.2	0.9 ± 0.1	6.1 ± 3.1	1.5 ± 0.2	0.20	<0.001
Volume, 10^3 m^2	1821.6 ± 780.9	57.1 ± 29.6	5.1 ± 1.3	554.1 ± 235.2	67.5 ± 27.5	0.21	<0.001
Mean depth, m	1.6 ± 0.3	0.5 ± 0.1	0.3 ± 0.0	2.2 ± 1.1	0.5 ± 0.1	0.22	<0.001
Max length, m	944.8 ± 194.4	340.1 ± 50.9	192.3 ± 16.4	1131.6 ± 170.7	373.3 ± 51.1	0.17	<0.001
Max width, m	220.5 ± 42.6	75.1 ± 10.9	54.1 ± 5.7	330.8 ± 96.9	74.4 ± 7.9	0.15	<0.001
Mean width, m	143.0 ± 26.5	53.2 ± 6.9	32.6 ± 3.2	241.2 ± 11.5	47.9 ± 5.7	0.17	<0.001
Major axis, m	1335.6 ± 270.5	526.2 ± 72.6	315.5 ± 35.0	2125.0 ± 1002.0	551.5 ± 78.0	0.14	<0.001
Minor axis, m	571.3 ± 119.0	189.3 ± 26.3	124.3 ± 12.8	1170.9 ± 449.9	180.8 ± 20.3	0.16	<0.001
Axis ratio	0.5 ± 0.1	0.4 ± 0.1	0.5 ± 0.1	0.7 ± 0.2	0.4 ± 0.1	0.03	0.03
Fetch	238.8 ± 42.3	81.8 ± 12.9	50.6 ± 5.6	348.5 ± 138.3	66.7 ± 8.4	0.17	<0.001

Morphometric characteristics of water bodies depending on the water body types. Channels and isolated floodplain lakes were located closest to the Dnipro River bed (planned comparison F = 15.7, P < 0.001, Table 2). Floodplain lakes were located farthest away, and bays were located in a transitional position. The types of water bodies did not differ in terms of the elevation of the surrounding terrain. The lowest variability of relief altitude was in the surroundings of isolated and confluent lakes (planned comparison F = 10.9, P < 0.001). Contrafluent lakes occupy a transitional position, and in other water bodies the variability of relief was the greatest (planned comparison F = 4.0, P = 0.05). Channels possess the largest surface area (planned comparison F = 17.2, P < 0.001), other types of water bodies do not differ by this indicator (planned comparison F = 0.009, P = 0.92). The greatest development of shorelines has been recorded for channels and contrafluent lakes (planned comparison F = 44.3, P < 0.001). Other types of water bodies did not differ from each other by this indicator (planned comparison F = 1.7, P = 0.19). The smallest axis ratio was for the channels (planned comparison F = 7.2, P < 0.001). Other types of water bodies did not differ statistically significantly by this indicator (planned comparison F = 3.0, P = 0.08).

Factor analysis of morphometric traits of water bodies. Three factors with eigenvalues greater than unity were extracted as a result of the factor analysis of morphometric traits of water bodies (Table 3). These three factors explain 85.8% of the cumulative correlation of morphometric features. Factor 1 reflects a latent variable that can be identified as the total size of the ponds. The total size of the water bodies was the largest for the Orilsky Canal, with slightly smaller sizes in the water bodies of the Dnipro riverbed. The smallest water bodies were in the Obukhivka ledge system. Factor 2 can be identified as a latent variable as the level of shoreline development. The water bodies of different systems did not differ by this indicator (F = 0.10, P = 0.74). Factor 3 can be identified as the altitude and variability of the terrain surrounding the water bodies. The lowest values of this factor were for the water bodies of the Orilsky Canal and the Obukhivka ledge system. The values were slightly higher for the water bodies of the Taromske and Mykolaivka ledge systems. The highest levels of relief and its variability were characteristic of the areas close to the water bodies of the Dnipro riverbed system.

Cluster analysis of water bodies by morphometric traits. Channels account for 27.8% of the total number of water bodies and 76.2% by area. Bays account for 18.2% and 6.3% by area, confluent lakes account for 8.3% by number and 3.2% by area, contrafluent lakes account for 15.6% by number and 4.7% by area, contrafluent-confluent lakes account for 11.9% by number and 8.0% by area, and isolated floodplain lakes account for 18.2% by number and 1.6% by area. Naturally, the number of channels is highest in the Dnipro River channel system and in the Orilsky Canal (42.6% and 50.0%, respectively). The density of canals is highest in the Obukhivka ledge system (28.4%) and in the Mykolaivka ledge system (24.6%). Accordingly, the lowest density of channels was observed in the Taromske ledge system (20.6%). The bay is a part of the Orilsky Canal and formally accounts for 50% of the number of water bodies. The smallest number of bays is characteristic of the Obukhivka ledge system (14.8%). In other systems, the proportion of bays is 18.0–20.4% of the number of water bodies. Among the natural systems, the proportion of isolated lakes was the smallest among the water bodies of the Dnipro River system (7.4%). The most common isolated lakes were found among the water bodies of the Mykolaivka ledge system (26.2%). A somewhat smaller proportion of this type of water body was in the Taromske ledge system (20.6%), and the smallest was in the Obukhivka ledge system (17.0%). Contrafluent and contrafluent-confluent lakes were most common in the Obukhivka ledge system, and contrafluent lakes were most common in the Taromske ledge system.

Table 2
Descriptive statistics of morphometric characteristics of water bodies depending on the types of water bodies

Variable	Channel, N = 84	Contrafluent lake, N = 47	Confluent lake, N = 25	Contrafluent-confluent lake, N = 36	Bay, N = 55	Isolated floodplain lakes, N = 55	R^2	*P*
Dist_Dnipro, km	1.3 ± 0.1	1.7 ± 0.1	1.7 ± 0.2	1.8 ± 0.1	1.5 ± 0.1	1.4 ± 0.1	0.06	<0.001
Mean relief altitude within the buffer, m	54.0 ± 0.3	53.8 ± 0.3	53.4 ± 0.5	53.7 ± 0.4	53.8 ± 0.3	53.8 ± 0.3	0.00	0.910
SD relief altitude within the buffer	2.3 ± 0.1	2.0 ± 0.1	1.8 ± 0.1	2.3 ± 0.1	2.1 ± 0.1	1.9 ± 0.1	0.06	<0.001
Surface area, ha	24.4 ± 8.0	2.7 ± 0.9	3.5 ± 2.1	6.0 ± 1.0	3.1 ± 1.5	0.8 ± 0.2	0.12	<0.001
Shoreline length, km	2.3 ± 0.4	1.1 ± 0.2	0.8 ± 0.3	1.7 ± 0.2	0.8 ± 0.2	0.5 ± 0.1	0.15	<0.001
Shoreline development	2.7 ± 0.1	2.4 ± 0.1	1.9 ± 0.1	2.1 ± 0.1	2.0 ± 0.1	1.8 ± 0.1	0.19	<0.001
Max depth	2.4 ± 0.5	1.6 ± 0.2	1.5 ± 0.5	3.1 ± 0.3	1.4 ± 0.2	1.3 ± 0.3	0.13	<0.001
Volume, thousand cubic meters	1181.4 ± 509.7	36.4 ± 21.4	94.8 ± 64.8	86.1 ± 19.4	52.6 ± 28.7	11.7 ± 7.3	0.12	<0.001
Mean depth	0.8 ± 0.2	0.5 ± 0.1	0.5 ± 0.2	1.0 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.10	<0.001
Max length	713.8 ± 138.7	326.4 ± 40.4	236.1 ± 53.4	572.0 ± 65.5	267.8 ± 42.1	193.5 ± 22.9	0.13	<0.001
Max width	146.3 ± 28.8	77.9 ± 10.1	77.5 ± 25.4	139.1 ± 11.6	72.0 ± 13.7	41.1 ± 4.1	0.13	<0.001
Mean width	95.5 ± 18.0	51.8 ± 6.8	50.8 ± 18.9	86.0 ± 6.9	44.9 ± 8.7	30.3 ± 3.0	0.11	<0.001
Major axis	1134.0 ± 194.7	521.3 ± 67.2	302.1 ± 70.0	783.8 ± 92.1	363.8 ± 58.7	258.2 ± 32.4	0.16	<0.001
Minor axis	396.9 ± 76.8	197.4 ± 24.1	157.5 ± 50.3	325.0 ± 36.0	177.3 ± 52.2	94.8 ± 9.5	0.14	<0.001
Axis ratio	0.4 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.07	0.080
Fetch	150.1 ± 29.2	65.6 ± 10.1	76.7 ± 27.7	148.8 ± 14.6	71.7 ± 14.0	47.2 ± 6.6	0.11	<0.001

Table 3
Factor analysis of morphometric traits of water bodies (varimax rotation) and discriminant analysis of clusters based on morphometric traits (data were log-transformed previously)

Variable	Factor analysis			Discriminant analysis			
	F1, λ = 10.3, 64.4 %	F2, λ = 2.0, 12.2 %	F3, λ = 1.5, 9.1 %	Root 1, λ = 2.9	Root 2, λ = 0.5	Root 3, λ = 0.2	Root 4, λ = 0.1
Dist_Dnipro, km	–0.17	–	–0.81	–0.35	–0.39	–0.35	–0.50
Mean relief altitude within the buffer, m	0.17	–	0.81	0.33	0.15	–	0.62
SD relief altitude within the buffer	0.49	–	0.54	0.59	0.21	–	–
Surface area, ha	0.97	0.19	0.12	0.96	–	–	–
Shoreline length, km	0.88	0.44	–	0.89	–	–0.21	–
Shoreline development	0.16	0.85	–	0.22	0.50	–0.44	–
Max depth	0.92	–0.14	0.23	0.88	–0.36	–	0.15
Volume, thousand cubic meters	0.98	–	0.17	0.97	–0.17	–	–
Mean depth	0.92	–0.20	0.25	0.91	–0.31	–	–
Max length	0.87	0.36	0.16	0.86	–	–0.18	–
Max width	0.97	–	–	0.95	–0.16	–	–
Mean width	0.98	–	–	0.96	–0.18	–	–
Major axis	0.82	0.54	0.12	0.85	0.18	–0.24	–
Minor axis	0.95	0.14	–	0.92	–	–0.18	–
Axis ratio	0.17	–0.79	–0.15	–	–0.43	0.23	–
Fetch	0.91	–0.12	0.15	0.92	–0.20	–	–

The cluster analysis allowed to us identify seven relatively homogeneous clusters in terms of morphometric traits (Fig. 2). These clusters can be differentiated by the results of discriminant analysis (Table 3).

The size of the water bodies, the development of the shoreline, and the height of the terrain surrounding the water bodies are important aspects of morphological differentiation. The identified clusters correspond well to the types of water bodies, which are identified based on their orientation relative to the preferred direction of water flow (Fig. 3). Contrafluent lakes correspond to cluster 5, confluent lakes correspond to cluster 4, contrafluent-confluent lakes correspond to cluster 2, and isolated floodplain lakes correspond to cluster 3. It should be noted that channels correspond to clusters 1, 6, and 7. The bay water body type does not have a clear correspondence among the clusters and is located between clusters 1 and 3. Clusters 1, 6, and 7 are located along the gradient of water body sizes (Root 1), which can be interpreted as the channel group of water bodies uniting water bodies of different sizes. In turn, these clusters occupy a similar position along the gradient of shoreline development (Root 1), which can be interpreted as meaning that the water bodies of the channel group have a high level of shoreline development in contrast to all other reservoirs. The contrafluent-confluent lakes (cluster 2) have the opposite character by this indicator: they have the least developed shoreline.

Vegetation structure in the surrounding area of water bodies. 15 types of vegetation cover within the reserve were identified based on the satellite image classification (Fig. 4). The water bodies have specific spectrums of the main types of plant communities in their surroundings. The isolated floodplain lakes differed from other types of water bodies in having a statistically significantly smaller area of shoreline shallow water free of aquatic macrophytes (planned comparison F = 17.0, P < 0.001, Table 4). Contrafluent and confluent lakes differed from channels, contrafluent-confluent lakes, and bays in having a smaller area of shoreline shallow water free of aquatic macrophytes (planned comparison F = 9.9, P = 0.047). The isolated floodplain lakes also had the lowest density of cattails in the surroundings of these water bodies compared to the others (planned comparison F = 20.5, P < 0.001). In turn, contrafluent and confluent lakes differed from all other water bodies in having a lower density of cattails (planned comparison F = 5.6, P = 0.015). The lowest density of reed beds was characteristic of isolated floodplain lakes (planned comparison F = 40.4, P < 0.001), contrafluent lakes occupied an intermediate position in this indicator (planned comparison F = 9.4, P < 0.002), and all other types of water bodies did not differ in terms of reed bed density (planned comparison F = 1.0, P = 0.31).

Sandy steppe had statistically significantly less projective cover surrounding contrafluent lakes, channels, and isolated floodplain lakes than surrounding other water body types (planned comparison F = 5.5, P = 0.02). The proportion of areas with macrophyte-free sandy bottoms was statistically significantly higher in the surroundings of channels (planned comparison F = 4.1, P = 0.042). Shrubs were most commonly found in the vicinity of confluent and lake contrafluent-confluent lakes (planned comparison F = 13.0, P < 0.001). Water bodies did not differ in the proportion of sparse forests in their surroundings. The proportion of dry meadows was the highest in the surroundings of isolated floodplain lakes (planned comparison F = 32.5, P < 0.001).

Other water bodies do not differ in the proportion of dry meadows in their surroundings (planned comparison F = 2.4, P = 0.12). In turn, the proportion of wet meadows was the lowest in the surroundings of isolated floodplain lakes (planned comparison F = 64.5, P < 0.001), whereas in the vicinity of contrafluent-confluent lakes and bays this type of vegetation was most common (planned comparison F = 9.8, P < 0.002). Oak forests were most often found in the vicinity of isolated floodplain lakes (planned comparison F = 22.9, P < 0.001). Contrafluent lakes were in a transitional position in this indicator (planned comparison F = 3.7, P = 0.05). Also, poplar forests were most often found in the surroundings of isolated floodplain lakes (planned comparison F = 39.3, P < 0.001). Wet and dry sandy meadows were found most often in the surroundings of isolated floodplain lakes (planned comparison F = 46.4, P < 0.001 and F = 24.2, P < 0.001 correspondently).

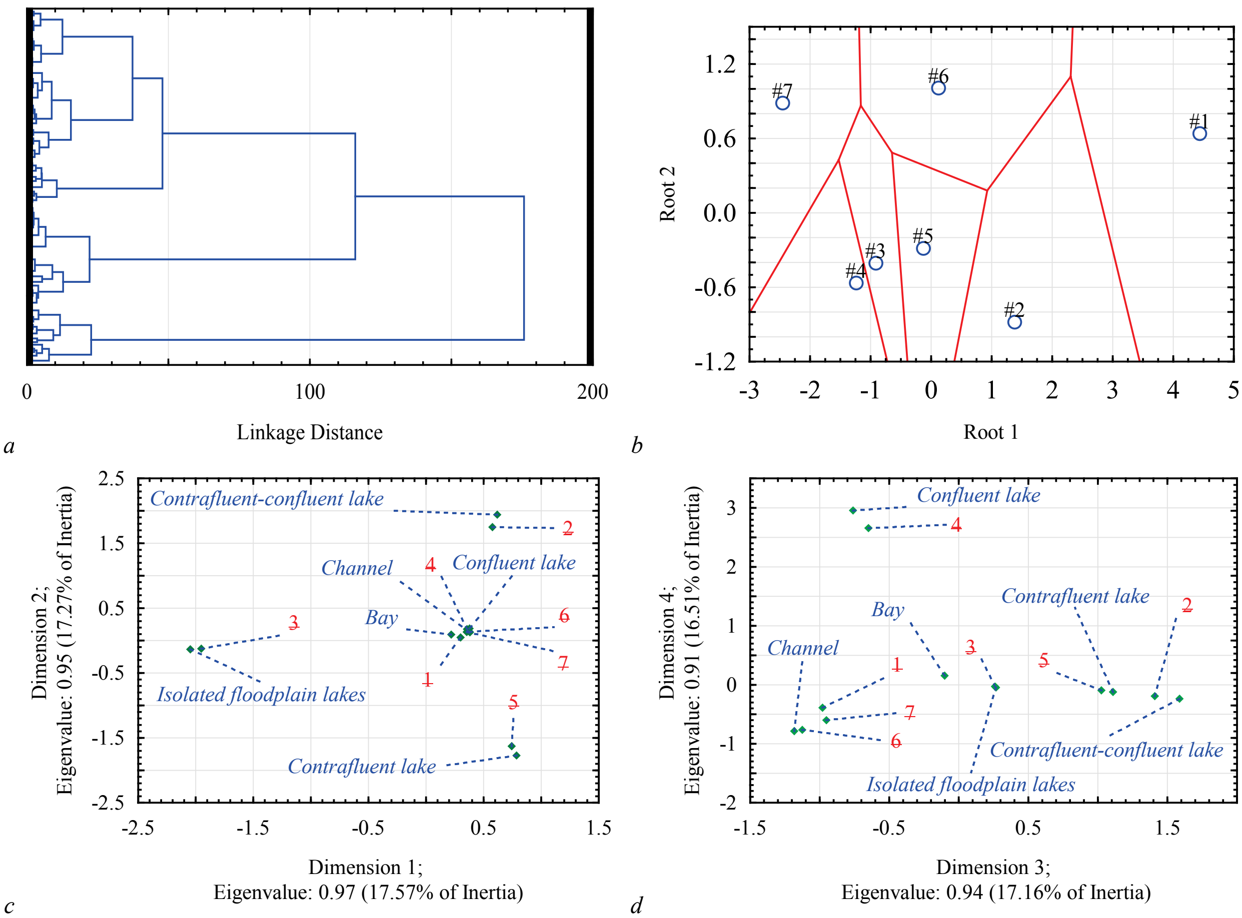

Fig. 2. Cluster analysis of water bodies based on the morphometric traits (*a*), discriminant analysis of clusters based on the morphometric traits of water bodies (*b*) and multiple correspondence analysis of clusters and types of water bodies (*c*, *d*): cluster analysis (Euclidean distance, Ward's method) identified 7 clusters, which are marked with a vertical red dashed-dotted line; Voronoi diagram of cluster location in the space of discriminant function 1 (abscissa axis, λ = 2.9, Wilk's lambda = 0.86, P < 0.001) and function 2 (abscissa axis, λ = 0.5, Wilk's lambda = 0.56, P < 0.001), multiple correspondence analysis allowed to identify the correlation between the selected clusters and types of water bodies

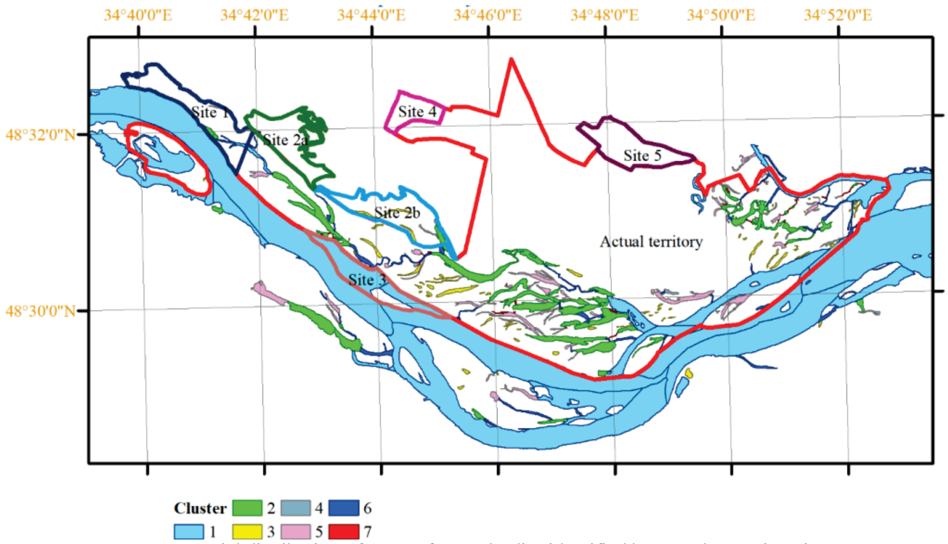

Fig. 3. Spatial distribution of types of water bodies identified by morphometric traits

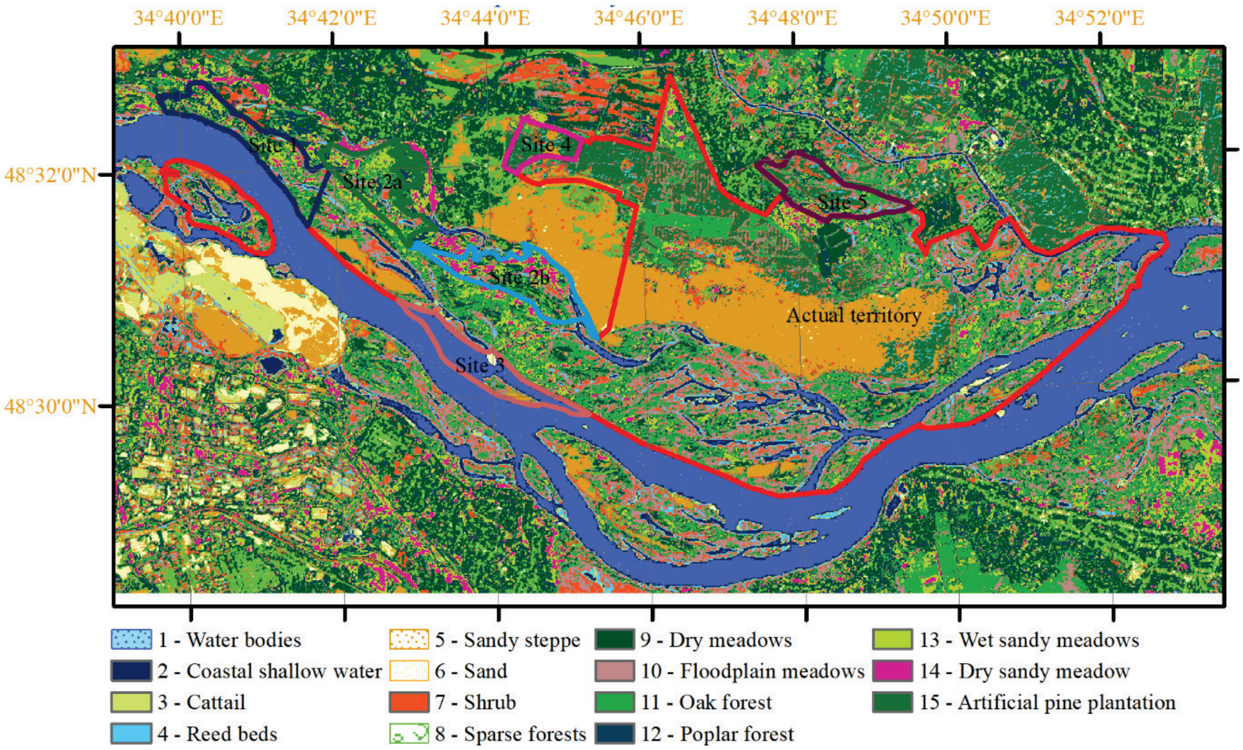

Fig. 4. Spatial distribution of vegetation types within the Reserve

Table 4
Descriptive statistics of the vegetation cover structure in the 100-meter buffer zone around water bodies (in % of the total projective cover)

Variable	Channel, N = 84	Contrafluent lake, N = 47	Confluent lake, N = 25	Contrafluent-confluent lake, N = 36	Bay, N = 55	Isolated floodplain lakes, N = 55	R^2	*P*
Coastal shallow water	1.7 ± 0.2	0.9 ± 0.2	1.2 ± 0.5	1.6 ± 0.4	1.4 ± 0.3	0.2 ± 0.1	0.08	<0.001
Cattail	2.1 ± 0.2	1.2 ± 0.3	1.6 ± 0.4	2.0 ± 0.3	2.2 ± 0.3	0.5 ± 0.1	0.10	<0.001
Reed beds	8.5 ± 0.5	6.0 ± 0.7	8.7 ± 1.0	9.0 ± 0.7	7.6 ± 0.8	3.2 ± 0.6	0.15	<0.001
Sandy steppe	0.8 ± 0.3	1.0 ± 0.5	2.3 ± 1.4	2.6 ± 1.2	2.0 ± 0.9	0.7 ± 0.4	0.02	0.30
Sand	0.8 ± 0.4	0.5 ± 0.4	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.02	0.40
Shrub	11.4 ± 0.7	10.4 ± 0.8	12.8 ± 1.3	13.6 ± 0.9	11.8 ± 1.0	6.5 ± 0.7	0.12	<0.001
Sparse forests	2.1 ± 0.6	2.2 ± 0.6	2.8 ± 1.1	0.9 ± 0.2	1.5 ± 0.5	2.3 ± 0.5	0.02	0.46
Dry meadows	2.4 ± 0.4	3.5 ± 0.7	2.5 ± 0.7	1.3 ± 0.3	2.1 ± 0.5	6.3 ± 0.9	0.11	<0.001
Floodplain meadows	30.8 ± 1.2	29.1 ± 1.3	28.1 ± 2.0	34.9 ± 1.5	32.8 ± 1.4	18.6 ± 1.5	0.21	<0.001
Oak forest	25.4 ± 1.1	29.3 ± 1.5	26.1 ± 2.5	24.4 ± 1.5	26.9 ± 1.8	34.7 ± 1.8	0.09	<0.001
Poplar forest	8.5 ± 0.6	9.1 ± 0.8	7.9 ± 1.3	6.5 ± 0.7	7.6 ± 0.8	13.4 ± 0.9	0.13	<0.001
Wet sandy meadows	4.9 ± 0.7	5.9 ± 1.0	5.6 ± 1.5	3.0 ± 0.6	3.4 ± 0.6	11.4 ± 1.3	0.16	<0.001
Dry sandy meadow	0.7 ± 0.2	0.9 ± 0.3	0.5 ± 0.2	0.2 ± 0.1	0.5 ± 0.2	2.0 ± 0.5	0.08	<0.001

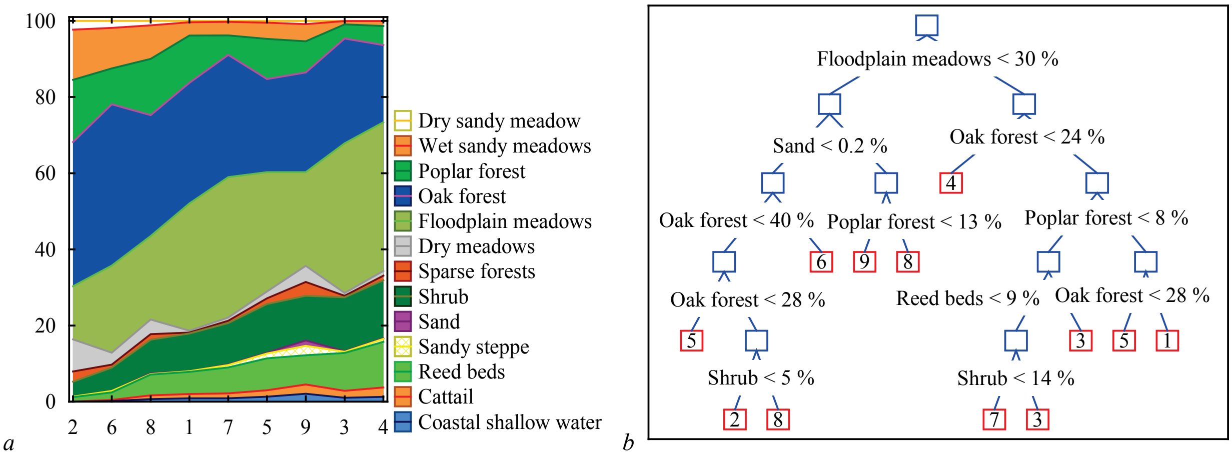

Fig. 5. Vegetation structure in nine clusters identified by cluster analysis of vegetation cover in the 100-meter buffer zone of water bodies (types of plant complexes in the buffer zone of water bodies) (*a*): the abscissa is the clusters ranked in the gradient of the highest variability based on the results of the principal component analysis, and the ordinate is the share of the plant community type in the vegetation cover structure; classification tree for determining types of plant complexes; predictive importance of indicators (0 = low importance; 100 = high importance): coastal shallow water – 33, cattail – 41, reed beds – 75, sandy steppe – 43, sand – 35, shrub – 72, sparse forests – 38, dry meadows – 37, floodplain meadows – 74, oak forest – 100, poplar forest – 81, wet sandy meadows – 69, dry sandy meadow – 46

Classification of water bodies based on the structure of the surrounding plant complexes. Nine clusters were identified as a result of the cluster analysis of water bodies based on the surrounding structure of vegetation complexes (Fig. 5). Each cluster includes the entire list of vegetation types that have been established for floodplain ecosystems. The peculiarity of the complexes is the specific relationship between different vegetation types. The most important structural factors that distinguish the complexes are the projective cover of oaks, floodplain meadows, and shrubs. At the top level of the hierarchy, the complexes are differentiated by the projective cover of floodplain meadows. At a lower level, the differentiation is based on the projective cover of sands or oaks. The clusters identified on the basis of plant complexes and morphometric traits, as well as the types of water bodies in terms of orientation relative to the preferred water flows, correspond to each other to some extent (Fig. 6). Thus, contrafluent-confluent lakes correspond to morphological cluster 2 and vegetation cluster 4. This indicates that in the vicinity of a contrafluent-confluent lake, floodplain meadows are found with a cover of at least 30%, and the projective cover of oak forests does not exceed 24%. Isolated floodplain lakes correspond to morphological cluster 3 and vegetation clusters 2 and 6. Thus, isolated floodplain lakes are usually surrounded by the vegetation complexes in which the projected coverage of floodplain meadows does not exceed 30%, the projective cover of sand does not exceed 0.2%, oaks either exceed 40% or not less than 28%, but shrubs occur on no more than 5% of the territory. Channels are most often surrounded by the plant complexes of cluster 9. They are characterized by a relatively low cover of floodplain meadows and poplar forests, but a high cover of sand. For other types of water bodies, associations with a limited list of vegetation complexes have not been found.

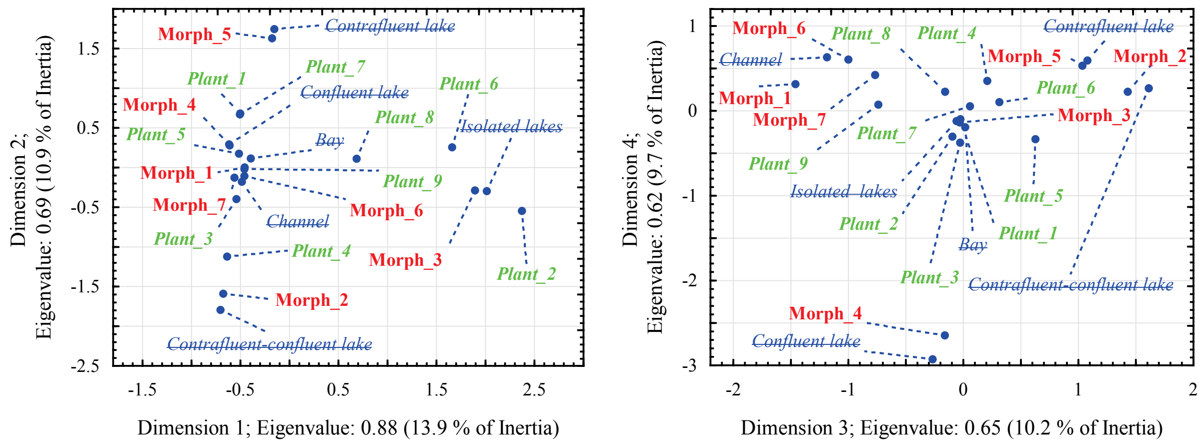

Fig. 6. Multiple correspondence analysis of water body types according to their orientation in relation to the prevailing direction of water flow (contrafluent lake, confluent lake, channel, contrafluent-confluent lake, bay, isolated floodplain lakes), water body types identified on the basis of morphometric characteristics (Morph 1–7), and types of plant complexes (Plant 1–9)

Discussion

The Dnipro River floodplain within the Dnipro-Orilsky Nature Reserve is home to a wide variety of water body types. They differ in their functional and morphological characteristics. The main morphological aspects of water bodies are their size, shoreline shape, and the surrounding terrain. Aspects of functional diversity are the preferred directions of water flow in water bodies, which indicates the ability for water exchange in them. In channels, water exchange always occurs, while in bays water exchange is very active. Contrafluent-confluent lakes are close to channels in terms of functional features, but water exchange is somewhat slower in them. In confluent lakes, the inflow component prevails, and in contrafluent lakes, the outflow component of water exchange prevails. In isolated lakes, there is no water exchange and it is possible only through groundwater or under conditions of significant flooding. Obviously, the different functional types of water bodies represent different stages of their genesis. The basic type is a channel. If water exchange in the channel is reduced, it may cross the channel and form contrafluent-confluent lakes. Depending on the loss of connection with the main river channel, this type of lake can turn into either a confluent lake or a contrafluent lake. It is likely that isolated lakes have independent genesis. There is also evidence that isolated floodplain lakes have greater ecological heterogeneity than connected lakes (Quirino et al., 2019). Allochthonous processes, such as nutrient and sediment inputs during high water, dominate connected parts of the floodplain. In contrast, autochthonous processes, such as phosphorus release from sediments and internal eutrophication, dominate isolated parts. These conditions also affect the dominant primary producers, biodiversity, and the degree of floodplain degradation, which in turn affects the potential viability of aquatic habitats (Reckendorfer et al., 2013). Zooplankton diversity and density are higher in a connected lake compared to an isolated lake (Napiórkowski et al., 2019). This is because connectivity is the reason why ecological processes and biological communities tend to be more similar between the individual habitats that make up a river-floodplain system (Thomaz et al., 2007). Our findings indicate that various functional types of lakes have their own morphological specificity and that the morphological types of water bodies identified by an independent procedure correspond quite well to the functional types. It should be noted that channels correspond to three morphological types, which differ significantly in size. The bay as a functional type does not have unambiguous morphological equivalents, apparently due to the considerable dynamism of the conditions where this type is formed. In terms of morphology, bays occupy a transitional position between channels and isolated lakes.

The variability in the altitude of the terrain surrounding the water body has been shown to be positively correlated with the depth of the water body. Obviously, the hills that form the variable relief in the floodplain were created by sandy sediments due to intense fluvial processes. The more flattened relief is created by sediments with a higher content of clay fractions. The deposition of clay fractions is possible when water exchange processes slow down. The relationship between the functional types of water bodies and the variability of the relief fully confirms this theory. Isolated lakes and confluent lakes are formed under conditions of the lowest variability of the surrounding relief, which can be seen as a consequence of the decay of the intensity of sedimentation of suspended particles during floods and as a result of a decrease in the intensity of water exchange. Channels and contrafluent-confluent lakes are formed under conditions of a significant level of variability of the surrounding relief, which emphasizes their significant water exchange capacity. The maximum terrain variability is observed in the area closest to the Dnipro River channel, and the variability decreases with distance from the channel.

Floodplain water bodies are also typified by the composition of the surrounding vegetation (Yorkina et al., 2022). The intensity of fluvial processes, geomorphological features, soil texture, nutrient supply, and moisture regime are environmental filters that affect the structure of plant communities (Yakovenko et al., 2023). In turn, plant communities affect the functioning of water bodies by regulating the intensity of erosion processes, affecting sedimentation processes and evaporation of water from the soil (Goulden et al., 2007). The specificity of plant complexes is in the quantitative ratio of their components. The predominance of certain components in plant complexes confirms the assumption of the functional role of different types of reservoirs. For example, the proportion of reed beds was highest in channels and contrafluent-confluent lakes. *Phragmites australis* (Cav.) Trin. and Steud is able to exist in a wide range of floodplain conditions and flow velocities (Hellings & Gallagher, 1992). Common reed can tolerate water depths up to 2 m, although the average growth depth of this species is ~ 45 cm (Coops et al., 1996). A decrease in water level has a positive effect on plants, which is expressed in an increase in their assimilation area (Squires & Valk, 1992). Experiments demonstrate that even low densities of *Ph. australis* can significantly impact turbulence and water quality. (Horppila et al., 2013). Aquatic macrophyte species exhibit a distinct zonation pattern in response to water depth and current speed. *Phragmites australis* is typically found in shallow water with slower currents compared to *Typha angustifolia* and *Zizania latifolia*, which share similar preferences (Asaeda et al., 2005). The presence of *Ph. australis* aggregations in a channel causes an increase in water depth in front of the obstacle and a reduction in average velocity. These changes are distributed unevenly across the cross-section, resulting in increased flow velocity and the formation of turbulent vortex movements. This generates a strong transverse shear stress that affects water transport capacity and channel formation processes (Wolski & Tymiński, 2020). Turbulence levels increase outside the reed beds but decrease with depth into the community (Zhukov et al., 2022). This turbulence contributes to the growth of surface dissolved oxygen, which is negatively correlated with reed density. Additionally, water turbulence affects the composition of bottom sediments, with coarse particle content increasing with turbulence. Low turbulence allows for the accumulation of organic matter and fine particles in anoxic sediments (Atapaththu et al., 2017). Thus, a significant intensity of water exchange with a high level of water level variability creates favorable conditions for the development of *Ph. australis* thickets. On the other hand, these thickets affect the dynamics of fluvial processes and create specific environmental conditions through the impact on water flow turbulence and the influence on the redistribution of suspended particles, oxygen and nutrient supply regimes.

The cattail thickets are represented by *Typha latifolia* L., *T. angustifolia* L., *T. laxmannii* Lepech. and *Zizania latifolia* (Griseb.) Stapf. Cattail (genus *Typha*) is an important component of wetland (reed) vegetation worldwide, especially in temperate zones (Smith, 1987). These macrophytes typically prefer slower water velocities and less water level variability, so they are most commonly found in bays. Cattail is well adapted to the rapid colonisation of bare soils in newly formed water bodies (Shipley et al., 1989). The distribution of vortices, areas of calm or fast flow, and velocity fluctuations has an impact on the biotic environment, which in turn affects the species composition, number, and diversity of plants (Kiraga et al., 2023). The height of *Typha* species increases as water depth increases. As water depth increases, the frequency of flowering and density of shoots decrease (Grace, 1989). A stable and low water level is beneficial for the germination of rhizome buds and the early growth of *Typha*. A rapid increase in water level during early summer promotes stem elongation (Yang et al., 2019). The growth rate of *Typha* was higher where the water level was shallow than where they were in deep water (Boers & Zedler, 2008). *Phragmites australis* and *Typha angustifolia* exhibit a distinct zonation in relation to water depth, with *Ph. australis* occupying shallower areas compared to *T. angustifolia* (Song, 2021). The biomass of *Typha* species was revealed to decrease only at a depth of more than 85 cm (Waters & Shay, 1992). The differentiation of *Phragmites* and *Typha* stands by depth was also confirmed by the results of our studies. Thus, the average depth of water bodies weighted by the projective cover of *Phragmites* was 0.70 ± 0.02 m, and the weighted by the projective cover of *Typha* was 1.00 ± 0.06 m.

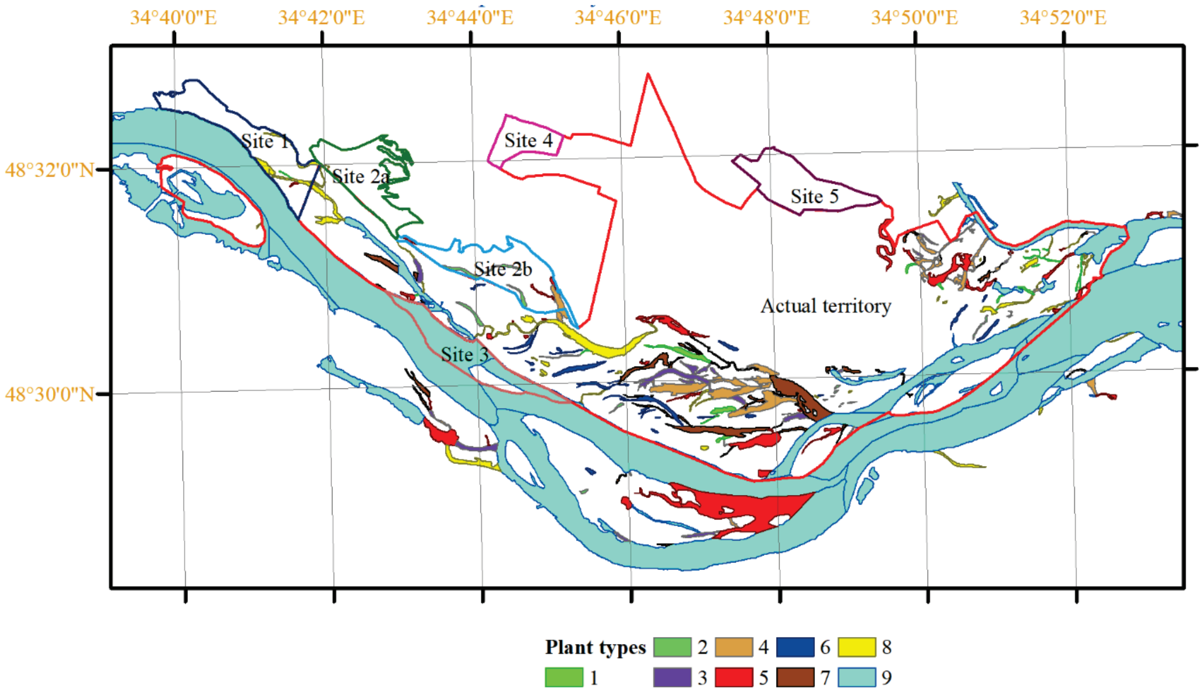

Fig. 7. Spatial distribution of water body types, identified on the basis of the complex of vegetation types surrounding the water bodies

The proportion of shallow shoreline waters with little sandy bottom vegetation cover is a good indicator of water flow velocity. That is why the proportion of this type of vegetation cover is highest in channels and contrafluent-confluent lakes, somewhat lower in bays and other lake types, and lowest in isolated lakes. Current velocity is an important factor that regulates the biomass of aquatic macrophytes in running waters. Even a relatively moderate increase in current velocity reduces the number of submerged aquatic plants (Chambers et al., 1991). The vegetation cover of shallow shoreline waters is usually represented by rheophilic plant species, such as some species of pondweed (*Potamogeton* sp.) in spring and the first half of summer, or water milfoil (*Myriophyllum* sp.) in the second half of summer and autumn. *P. crispus* prefers areas with high current velocity. Their highest occurrence was observed at average current velocities of 0.08–0.20 m/s and they clearly preferred depths of more than 80 cm (Ochs et al., 2018). *Myriophyllum* species can significantly affect the water flow rate and turbulence phenomena (Przyborowski et al., 2019). *Myriophyllum aquaticum* shows a strong preference for low flow, inhabiting only areas of relatively slow velocity and shallow depth. At speeds above 0.10 m/s, this species is practically not found. The most suitable depths for *M. aquaticum* are 0–20 cm. This species is most often found on sandy substrates (Ochs et al., 2018). Sandbars are most often found in the vicinity of channels. They are formed as a result of the movement of suspended particles by high velocity water currents. The bottom material was transported both as a suspension and as a suspended stream. The downstream flow of sand grains consists of both local material and material coming from the catchment, with different transport pathways and dependence on flow conditions (Ramirez & Allison, 2013).

Sandy steppe was most often found surrounded by contrafluent-confluent lakes. This type of vegetation occurs on high sandy hills in a floodplain with a deep water table. The low capillary properties of sandy soils do not allow the water table to rise high in the soil profile, so the predominant source of water is precipitation or condensation water. Sandy soils are a good filter for water (Keesstra et al., 2012), and condensation water can be an additional source of water for floodplain lakes (Yakovenko & Zhukov, 2021). Condensation water can also compensate for water lost through evaporation from the soil and is a key factor in maintaining the stability of sand dunes (Li, 2002). Thus, it can be assumed that steppe vegetation on sandy soils can be an indicator of specific conditions of water supply to water bodies, which affects their hydrological regime and water quality. The main source of water in floodplain water bodies is the Dnipro River channel, but alternative sources of water supply are also possible. The role of precipitation is proportional to the area of water bodies and the size of the local catchment area, which is small within the floodplain. The importance of groundwater can increase significantly as the water body approaches the second floodplain terrace, which is marked by the sandy steppe.

The genetic specificity of isolated lakes is underlined by the peculiarities of the surrounding vegetation (Zymaroieva et al., 2021). The surroundings of isolated lakes are dominated by dry and wet sandy meadows, poplar forests and oak woods, and much less vegetation types such as shrubs and wet floodplain meadows than those surrounding other water bodies. The isolated lakes can be assumed to be formed on the sandy riverbed berms of very ancient origin, which were also subjected to wind erosion. The isolated lakes occupy low relief areas with little variation in elevation in the surrounding area. That is, they are flattened areas of the floodplain. The flattened nature of the relief could have been formed under the influence of wind transport of sandy soils. The sandy nature of the soils indicates the importance of alluvial processes in the initial stages of the genesis of this floodplain area. The regional groundwater flow mainly supports the shallow groundwater of the floodplain wetlands. Floodplain wetlands are dynamic zones between the regional groundwater and the river, and the contrasting nature of the hydrological regime in the floodplain is due to the combination of regional groundwater flow and topography (Fu et al., 2020). Fluctuations in the water level of floodplain lakes are also known to be largely due to their connection with groundwater (Geest et al., 2005).

The use of information on the vegetation cover structure in the floodplain surrounding the water bodies clarifies the functional features of the water bodies and recreates the interrelationships in the floodplain as a holistic dynamic landscape. The classification units of water bodies are defined based on the structure of the surrounding vegetation. This provides additional information on genetic relationships and functional features identified by the morphological classification of water bodies. Information about the surrounding terrain is also important for understanding water bodies. The study analysed the water bodies' morphological features, specifically the average height of the surrounding relief and its variability.

For further investigations, it is of interest to provide a detailed geobotanical interpretation of the vegetation structure of individual typological units of lakes. This is important for understanding the flora of the water body and its surroundings. Remote sensing data enables the reproduction of temporal variability of the vegetation cover structure, revealing the connection between structural and dynamic features of water bodies in various floodplain regions. The study of eutrophication phenomena, depending on the typological features of floodplain water bodies, has significant practical implications.

Conclusions

The Dnipro-Orilsky Nature Reserve contains a diverse range of water bodies within its floodplain, including various functional and morphological types. Approximately a quarter of the floodplain is covered by these water bodies, which vary in size, shoreline shape, and surrounding relief features. The predominant directions of water flow within the bodies indicate their ability for water exchange, highlighting their functional diversity. Functional types correspond well to the water body types identified based on morphological criteria. The connected parts of the floodplain are dominated by allochthonous processes, such as nutrient and sediment inputs during high water, while the isolated parts are dominated by autochthonous processes, such as phosphorus release from sediments and internal eutrophication. The composition of the vegetation complexes surrounding floodplain water bodies also characterizes them. The structure of plant communities is affected by environmental filters such as the intensity of fluvial processes, geomorphological features, soil texture, nutrient supply, and moisture regime. This, in turn, impacts the functioning of water bodies by regulating erosion processes, sedimentation, and evaporation of water from the soil.

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