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Distribution and ecological growth conditions of *Utricularia australis* R. Br. in Ukraine

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Abstract

The study shows the biodiversity of *Utricularia australis* from western to northern regions of Ukraine. The environmental conditions of Ukraine are favourable for the spread and formation of phytocenosis involving *U. australis*, especially on thermoclimatic, cryothermal and continental scale. A broader range of the species' relation to humidity has been recorded. The research outcome shows the existence of the species in conditions from shallow, parched reservoirs to deep water habitats which allows the species to withstand temporary drying of reservoirs in summer periods. The resilience of *U. australis* to some water quality parameters, including nitrogen, phosphorus, iron content, colour, pH and organic contamination was higher than in previous studies and Tsyganov's ecological scales. Thus, due to its wide range of tolerance to the majority of environmental factors, *U. australis* tends to spread in contemporary climatic conditions in Ukraine. Considering that the species has category "vulnerable" in the country and is listed in the red data book of Ukraine, its conservation status is likely to be revised further.

Key words: environmental parameters, phytocenosis, tolerance, *Utricularia australis*, water quality

INTRODUCTION

Utricularia australis R. Br. is a rootless free-floating submerged aquatic carnivorous plant. It is widely distributed in temperate and tropical regions of the world, except North and South America, where in the majority of localities it is sterile [TAYLOR 1989]. Fruiting of the species takes place in several localities in China [TAYLOR 1989] and Europe [ASTUTI, PERUZZI 2018].

The hybrid origin of the sterile *Utricularia australis* R. Br. f. *australis* Komiya & Shibata is the result of asymmetric hybridization of two diploid fertile taxa – *Utricularia australis* R. Br. f. *tenuicaulis* Miki (mostly as female) and *Utricularia macrorrhiza* Le Conte (mostly as male). It has

been found growing in Japan [KAMEYAMA *et al.* 2005]. In Japan, where the hybridogenic species *Utricularia australis* f. *australis* and both parental species can be found growing, they never occur together in one locality. Most localities are dominated by the hybrid F₁ *Utricularia australis* f. *australis*. It is important that hybrid F₁ is sterile, so subsequent hybridizations do not occur. The researchers have presumed that the current spread of *Utricularia australis* f. *australis* is predominantly caused by ornithochorias – the transfer of vegetative diaspores of the species.

The transfer of the *U. australis* diaspores by water and coastal-water birds is passive to plumage and paws and involves separate parts of plants (parts of shoots, turions etc.) [KAMEYAMA *et al.* 2005; TAYLOR 1989]. In our opin-

ion, the passive transfer of *U. australis* seeds by these species is also not excluded. Until now, the question of origin of the Japanese *Utricularia australis* f. *australis* and the European *Utricularia australis* R. Br., as well as the cause of sterility of the latter, remains open for future study.

Data pertaining to the spread of *U. australis* in Europe are problematic because the species is habitually like *Utricularia vulgaris* L. and has been frequently confused with it [TAYLOR 1989]. In Europe, *U. australis* occurs in temperate, boreal and Mediterranean regions [UOTILA 2013].

It has been demonstrated that *U. australis* is characterized by high efficiency of re-utilization of some macronutrients from tissues of senescent shoots to the young actively growing parts. For nitrogen it reaches about 57%, and for phosphorus about 81% [ADAMEC 2002]. In addition, these properties combined with its ability to trap small aquatic animals and plants through bladder-like traps [ELLWOOD *et al.* 2019; KOLLER-PEROUTKA *et al.* 2015; METTE *et al.* 2000] for having an alternative source of nitrogen and phosphorus, allows the species to grow in wide range conditions, including poor oligotrophic and mesotrophic reservoirs. According to another study, *U. australis* grows well on an oligotrophic substrate, and the catch of insects does not compensate for the plant's need for all necessary elements except nitrogen, and the rest of the plant's nutritional elements are absorbed from other types of food: pollen, algae, etc. [KOLLER-PEROUTKA *et al.* 2015]. The role of phytoplankton as prey of *U. australis* was also noted [ELLWOOD *et al.* 2019]. There is also a wide range of species of small animals that are consumed by the *U. australis* depending on the habitat. These include cyclopoid copepodids, cladocerans, ostracods, and rotifers, and also insect larvae living in the aufwuchs and small autotrophic organisms [METTE *et al.* 2000]. Some sources note that utricularia seeds are located in the clade of the earliest node of the Utricularia. They are globose/ovoid in shape, mostly with reticulated testa and raised anticlinal walls [JOBSON *et al.* 2003]. Such a surface may allow seeds to remain afloat. It may support plant's dispersal by water birds [ELLISON, ADAMEC (eds.) 2018; TAYLOR 1989].

Also, the mucus secreted contributes to the fact that small parts of the plant can adhere to and be carried by waterfowl. *Utricularia australis* grows in Europe in many aquatic cenoses and forms its own association *Utricularietum australis* Th. Müller & Görs 1960 with a small number of species in which it is dominant with a projective coverage between 50 and 90%. This aquatic cenosis was first described in Germany. It was found in miry holes and peat extraction pits [MÜLLER, GÖRS 1960]. Later, numerous localities of this association were described in publications in Germany [HOFMANN 2001], Austria [SCHRATT 1993], Hungary [KÁRPÁTI 1963], Slovakia [OŤAHELOVA 1980], Czech Republic [SIROVÁ *et al.* 2014], Poland [OCHYRA 1985] and other countries. This association is also described to be present in various anthropogenic biotopes, such as ponds formed after peat extraction, fishponds, peaty ditches, etc. [MÜLLER 1977; PASSARGE 1996; VAHLE, PREISING 1990]. According to the research, this floristic association occurs in shallow (50–150 cm) oligo-

trophic or mesotrophic hollows in peat bogs with acidic water [SPAŁEK 2006]. In Poland, *U. australis* also was noted as a part of *Nupharo-Nymphaetum* [ŻUKOWSKI 1974] and in *Lemno minoris salvinietum natantis* associations [TOMASZEWICZ 1969] in slowly flowing waters. It also has been shown that the association of *Utricularietum australis* can form micromosaic complexes with other associations of aquatic vegetation, notably *Potametum natantis*, *Phragmitetum australis* and others [SPAŁEK 2006].

Since *U. australis* is a eurytopic species growing in a wide range of trophic water bodies, from oligotrophic and mesotrophic to eutrophic, the hydrochemical parameters in its habitats also vary significantly. In addition, major seasonal dynamics of salt content in water has been demonstrated for habitats of this species in Spain [RODRIGO, CALERO 2019].

Previous studies determined optimal values of the main hydrochemical parameters of the reservoirs in which *U. australis* grows [CIRUVANO *et al.* 1996; DÍTĚ *et al.* 2006; KIBRIYA, JONES 2007; KOSIBA 2004; SPAŁEK 2006; SIROVÁ *et al.* 2014].

Thus, for *U. australis* in western, central and southern Europe, localities of the species as well as their ecological conditions are well documented and studied. In Ukraine, the situation is different, since until recently this species has been cited only for Transcarpathia, while ecological parameters of its habitats in the region have remained unexplored.

The main objectives of this research include: 1. Study of the current growth and distribution of aquatic cenoses of *U. australis* in Ukraine; 2. Analysis of the main hydrochemical parameters of water bodies from the main habitats and aquatic cenoses of *U. australis* in Ukraine; 3. Determination of the ecological amplitude of this species in relation to environmental factors.

MATERIALS AND METHODS

The field studies were conducted on the plain of Ukraine, on the right bank of the Dnieper River in 2012–2019. TAYLOR [1989], and HUSÁK [2000] keys were used to determine and identify *U. australis*. Plant communities were studied according to the Braun–Blanquet approach [WESTHOFF, VAN DER MAAREL 1973], and phytosociological relevés are stored using the TURBOVEG software [HENNEKENS, SCHAMINÉE 2001]. Phytosociological nomenclature for eastern Europe has been given after ŠUMBEROVÁ *et al.* [2011], and it reflects characteristic features of Ukraine [IAKUSHENKO, BORYSOVA 2012]. In total, 46 relevés of coenoses with *U. australis* from 29 localities were carried out, and in the 18 most representative relevés, the main hydrochemical water parameters were studied (Tab. 1, 2).

Water quality at the observation points was evaluated by [ROMANENKO, ZHUKINSKIY 1998], according to which all analyses for determining water quality indicators were divided into three main blocks: 1. Block of water quality assessment according to the criteria of salt composition. This group includes indicators of water quality in terms of mineralization, sulphate and chloride content. 2. Block of

Table 1. Typical relevés with participation of *Utricularia australis* in Ukraine

No. relevé	6	33	3	32	4	34	9	10	14	7	12	8	11	16	18	1	2	19	26	37	38	40	41	42	44	
Number of species	11	7	15	15	6	1	8	5	7	11	7	8	10	10	11	6	7	9	7	7	6	3	3	7	5	
Water depth, cm	5	6	50	45	110	100	70	100	20	70	50	190	150	80	1	5	6	4	10	10	1	90	80	100	80	
Relevé square, m ²	20	25	4	4	4	12	9	9	4	9	12	9	25	4	4	4	4	4	4	25	8	4	4	4	4	
Projective cover of abovewater layer	46	50	29	35	11	0	10	81	56	78	100	55	25	49	45	36	41	31	28	70	22	0	70	15	11	
Projective cover of underwater layer	50	40	60	98	48	50	40	45	40	60	32	60	70	50	85	90	90	75	35	60	95	100	55	30	20	
<i>Utricularia australis</i>	4	3	3	3	3	4	3	3	3	3	2a	3	2b	3	3	4	4	3	3	4	5	4	4	3	2b	
<i>Agrostis stolonizans</i>																3	3	2b							2a	+
<i>Alisma-plantago-aquatica</i>	r		2a	2b				+							1										r	
<i>Batrachium circinatum</i>			2a	2b															2a							
<i>Bidens cernua</i>			1	2a																						
<i>Bidens frondosa</i>				+																		2a				
<i>Callitriche stagnalis</i>			+	+																						
<i>Carex acutiformis</i>				+																						
<i>Carex riparia</i>										3												+				
<i>Carex rostrata</i>	3	2a																								
<i>Ceratophyllum demersum</i>			2a				2a	2a			2b		2a	2a	2b								2a			
<i>Ceratophyllum submersum</i>				2a								2b														
<i>Chara globularis</i>																3	3	3					3		3	
<i>Cicuta virosa</i>									+					r												
<i>Eleocharis palustris</i>																				2a						
<i>Elodea canadensis</i>				+			2a			2b		2a		2a												
<i>Equisetum limosum</i>	2a	3								r											r					
<i>Glyceria fluitans</i>	1	r					+							2a					2a							
<i>Glyceria maxima</i>										r				+	2a											2a
<i>Glyceria plicata</i>			2a	2a																						
<i>Hottonia palustris</i>		1																								3
<i>Hydrocharis morsus-ranae</i>	1		2a	1	2a		1		2a	2a	1	2a		2a	3											2a
<i>Juncus articulatus</i>		r																1	+							
<i>Juncus bulbosus</i>		4																								
<i>Juncus conglomeratus</i>	r		r																	+						
<i>Lemna minor</i>			1	+	1		1		+	1	2a	2a	2a	2a	+	+	1	1	1						r	
<i>Lemna trisulca</i>			+		1		1			2a	2a	2a												2a		
<i>Lycopus europaeus</i>	r			r													r									
<i>Lysimachia vulgaris</i>									+													+				
<i>Lythrum salicaria</i>	r	r							1								r	r			r					
<i>Myriophyllum spicatum</i>			1										2b		2a											
<i>Najas marina</i>													2a													
<i>Naumburgia thyrsiflora</i>	1																									
<i>Nitella mucronata</i>			3	3																						
<i>Nuphar luteum</i>									2a		2b															
<i>Oenanthe aquatica</i>																				2a						
<i>Persicaria amphibia</i>																r										
<i>Persicaria hydropiper</i>														r							r					
<i>Phragmites australis</i>																		2a						4	2a	
<i>Poa palustris</i>	r																									
<i>Potamogeton acutifolius</i>															2b											
<i>Potamogeton berchtoldii</i>	+																									
<i>Potamogeton crispus</i>													2a													
<i>Potamogeton pectinatus</i>																									2b	
<i>Potamogeton perfoliatus</i>													2a													
<i>Potamogeton pusillus</i>																			2a							
<i>Potamogeton trichoides</i>			2a	2a																						
<i>Ranunculus flammula</i>				r																	r					
<i>Salvinia natans</i>							r			2a	2a		2b													
<i>Sparganium emersum</i>														2b												
<i>Spirodella polyrhiza</i>			r		1		1			1		2a	2a	2a	+			+								
<i>Stratiotes aloides</i>										4	5															
<i>Trapa natans</i>												2a														
<i>Typha angustifolia</i>								5																		
<i>Typha latifolia</i>		+																			r	2b				
<i>Typha laxmannii</i>																				2b						

Source: own study.

Table 2. Current geographical distribution *U. australis* localities in Ukraine

Source of information	Latitude	Longitude	Location description
1	2	3	4
Relevés No. 1–2	50.482972	28.907186	Zhytomyr oblast, Zhytomyr district, 0.5 km to the North from the village Barashivka, in the flooded depressions of bottom of the clay quarry (O. Orlov, 06.07.2014, KW). Relevé square – 4 m ²
Relevé No. 3	50.484314	29.018558	Zhytomyr oblast, Zhytomyr, western vicinity, Bohunia, small shallow water near pond in spent Bohuns'kiy granit quarry (O. Orlov, 27.07.2014, KW). Relevé square – 4 m ²
Relevé No. 4	50.321367	29.014289	Zhytomyr oblast, Korostyshiv district, eastern vicinity of Korostyshiv, forest pond Trete lake, in the water near dam, cenoses <i>Utricularietum australis</i> Müller et Görs 1960 (D. Iakushenko, 11.08.2016, KW). Relevé square – 4 m ²
Relevé No. 5	50.500064	29.264347	Zhytomyr oblast, Radomyshl' district, eastern vicinity of Radomyshl', in oxbow on the right bank of Teteriv River (O. Orlov, 16.07.2017, KW). Relevé square – 4 m ² .
Relevé No. 6	51.309636	28.751008	Zhytomyr oblast, Luhyny district, village Lypnyky, in artificial pond near office of Lypnycke forestry unit of «Luhynske State Forestry». In the coastal strip with 3 m width, in north-east pond part. Pond mezo-eutrophic (O. Orlov, 05.08.2014, KW). Relevé square – 20 m ²
Relevé No. 7	51.321483	29.167278	Zhytomyr oblast, Narodychi district, 0.8 km to the South from Narodychi, in closed oxbow in on the right bank of Uzh River, near the bank, in stagnant water, in the thicket of <i>Stratiotes aloides</i> , Nature Reserve «Drevlianskiy» (O. Orlov, 02.09.2016, KW). Relevé square – 3×3 m (9 m ²)
Relevé No. 8	51.215903	29.667203	Zhytomyr oblast, Narodychi district, 1 km above village Rozsohivs'ke, in reservoir on Uzh River, in weakly running water, Nature Reserve «Drevlianskiy» (O. Orlov, 01.09.2016, KW). Relevé square – 3×3 m (9 m ²)
Relevé No. 9	51.325106	29.162747	Zhytomyr oblast, Narodychi district, 0.7 km to the South from Narodychi, on the right bank of Uzh river, dominant in oxbow, Nature Reserve «Drevlianskiy» (O. Orlov, 07.07.2016, KW). Relevé square – 3×3 m (9 m ²)
Relevé No. 10	48.315222	25.081639	Chernivetska oblast, Kosiv district, Kosiv, salsuginous lake Bans'ke on the place of the former salt mining, near the bank, National Natural Park «Gutsulchshyna» (I. Danylyk, T. Solomaha, 20.07.2006, KW) [Danylyk, Solomaha, Solomaha, Tsymbaliuk, 2007]. Relevé square – 3×3 m (9 m ²)
Relevé No. 11	50.817631	29.402006	Zhytomyr oblast, Radomyshl' district, Radomyshl', in reservoir on the Myka River, near the bank (O.Orlov, 28.09.2014, KW No. 115896; O. Orlov, 02.08.2015, KW No. 115889). Relevé square – 5×5 m (25 m ²)
Relevé No. 12	48.214725	22.543325	Zakarpatska oblast, Beregovo district, Dyida village, natural boundary Touvar, in drainage channel with dense <i>Stratiotes aloides</i> (R. Kish, 13.09.2002). Relevé square – 3×4 m (12 m ²).
Relevé No. 13	50.696036	29.373911	Zhytomyr oblast, Radomyshl' district, 2 km to south-west from village Fedorivka, in small peat ditch near alder forest, on the open place (O. Orlov, 16.08.2014). Relevé square – 2×5 m (10 m ²)
Relevé No. 14	50.484222	28.088253	Zhytomyr oblast, Pulyny district, 1 km to the south-east from village Sokoliv, forest lake Chaikivske, in the water, coastal strip, amid <i>Carex riparia</i> , (O. Orlov, 03.07.2017, KW). Relevé square – 4 m ²
Relevé No. 15	51.092906	29.534036	Zhytomyr oblast, Radomyshl' district, 1 km to the North from village Medelivka, in the lake Buslove (O. Orlov, 03.08.2016, KW). Relevé square – 5×5 m (25 m ²)
Relevé No. 16	50.194364	29.233764	Zhytomyr oblast, Korostyshiv district, eastern vicinity of village Strucivka, in the wide drainage channel near the bridge, water flow is very weak (O. Orlov, 05.07.2019, KW). Relevé square – 4 m ²
Relevé No. 17	51.160386	27.882753	Zhytomyr oblast, Olevs'k district, between village Radovel and village Rudnia Radovels'ka, canalized river Perga (leg. M.F.Veselskiy, 08.09.2019; det. O. Orlov, 08.12.2019). Relevé square – 5×5 m (25 m ²)
Relevé No. 18	50.136161	27.739897	Forest-Steppe Zone, Zhytomyr oblast, Romaniv district, 2 km to the south-west from village Mala Kozara in fish pond, near dam (O. Orlov, 21.08.2018, KW). Relevé square – 4 m ² .
Relevés No. 19	50.482972	28.907186	Zhytomyr oblast, Zhytomyr district, 0.5 km to the north from village Barashivka, in the flooded depressions of bottom of the clay quarry (O. Orlov, 06.07.2014, KW). Relevé square – 4 m ² .
Relevé No. 32	50.484314	29.018558	Zhytomyr oblast, Zhytomyr, small shallow water near pond in spent Bohuns'kiy granit quarry (O. Orlov, 27.07.2014, KW). Relevé square – 4 m ² .
Relevé No. 33	51.044056	28.080861	Zhytomyr oblast, Luhyny district, village Lypnyky, in artificial pond near office of Lypnycke forestry unit of «Luhynske State Forestry». In the coastal strip with 4–5 m width, in western pond part, largely in the shade of old birch trees. Pond mezo-eutrophic (O. Orlov, 05.08.2014, KW). Relevé square – 5×5 m (25 m ²)
Relevé No. 34	51.044056	28.080861	Zhytomyr oblast, Luhyny district, village Lypnyky, in artificial pond near office of Lypnycke forestry unit of «Luhynske State Forestry». In open water in the central part of the pond. Pond mezo-eutrophic (O. Orlov, 05.08.2014, KW). Relevé square – 3×4 m (12 m ²)
Relevé No. 35	50.482972	28.907186	Zhytomyr oblast, Zhytomyr district, 0.5 km to the North from the village Barashivka, in the flooded depressions of bottom of the clay quarry (O. Orlov, 06.07.2014, KW). Relevé square – 6 m ²
Relevé No. 36	50.295819	29.060186	Zhytomyr oblast, Korostyshiv district, eastern vicinity of village Kyrychanka, in the wide drainage channel, 200 m from the bridge, water flow is very weak (D. Iakushenko, 19.07.2012! KW). Relevé square – 4 m ²
Relevé No. 37	51.044056	28.080861	Zhytomyr oblast, Luhyny district, «Luhynske State Forestry», Dyvlyn forestry unit, quarter No. 30, in shallow lake in former sand quarry together with <i>Juncus bulbosus</i> (O. Orlov, 01.09.2017, KW). Relevé square – 5×5 m (25 m ²)
Relevé No. 38–39	51.507886	25.4608	Volyn' oblast, Manevychi district, north-east vicinity of village Leshnivka, in watered roadside ditch (I. Danylyk, O. Kuziarin, L. Borsukevych, S. Sosnovska, 14.08.2017, LWKS). Relevé square – 2×4 m (8 m ²)
Relevés No. 40–43	48.315222	25.081639	Ivano-Frankivsk oblast, Kosiv district, Kosiv, Bans'ke lake (D. Iakushenko, I. Corney, 15.08.2016). Relevé square – 2×2 m (4 m ²)

continue Tab. 2.

1	2	3	4
Relevés No. 44–46	50.321367	29.014289	Zhytomyr oblast, Korostyshiv district, eastern vicinity of Korostyshiv, forest pond Trete lake, in the water near dam (D. Iakushenko, 10.08.2016). Relevé square – 4 m ²
According to the literature	49.897483	24.111222	Lviv oblast, Zhovkva district, near the city of Dublyany (Visyulina, 1961)
According to the literature	48.518994	22.332692	Zakarpatska oblast [Province of Transcarpathia], Uzhgorod district, village Velyki Heevtsi, floodplain of the Latorytsia River, Peresh tract, old lakes (B. Prots, 1997; R. Kish, 17.07.2003)
According to the herbarium GZU	48.433006	22.273117	Zakarpatska oblast [Province of Transcarpathia], Uzhgorod district, surroundings of the village of Chervone, Csaronda channel near the pumping station (R. Kish, 02.09.2003, GZU, No. 246447-246448)
According to the literature	48.466275	22.462097	Zakarpatska oblast [Province of Transcarpathia], Mukachevo district, near the village of Dragina (Prots, 2009)
According to the Ukrainian Biodiversity Information Network, without description	48.115783	23.148497	Zakarpatska oblast [Province of Transcarpathia], Vynohradiv district, Vynohradiv city (Vasily Gleba, 30.07.2016) (according to the Ukrainian Biodiversity Information Network http://www.ukrbin.com/show_image.php?imageid=139934)
According to the herbarium LWKS	51.451619	25.680817	Rivne oblast, Volodymyrets district, near the village of Berezina, reclamation canal in the floodplain of the Berezina River (I. Danylyk, 17.06.2019, LWKS)
According to the herbarium KW	51.324306	28.326644	Zhytomyr oblast, Ovruch district, 3.5 km south-west. from the Listvyn village, Slovechansky DLG, Listvynske forestry, apt. 57, ed. 9, in a pond in the woods, a strip in the water in front of the thickets of <i>Phragmites australis</i> (O. Orlov, 05.09.2018! KW)
According to the herbarium KW	51.337592	28.320581	Zhytomyr region, Ovruch district, 0.7 km south-west of the Listvyn village, Slovechansky DLG, Listvynske forestry, apt. 20, ed. 35, in a pond in the upper reaches of the Noryn River, many, coenosis <i>Utricularietum australis</i> Müller et Görs 1960 (O. Orlov, 05.09.2018! KW)
According to the herbarium KW	51.388531	28.024439	Zhytomyr region, Ovruch district, 4 km west. with. Kovanka, SE "Slovechanske LH", apt. 13, hydrological reserve Didove Lake, in the water, in many places (O. Orlov, 03.07.2019! KW)

Source: own study.

assessment of water quality by chemical saprobological criteria. This group includes indicators of water quality by oxygen regime, suspended solids, transparency, pH, ammonium nitrogen content, nitrates and nitrites, phosphorus phosphate and oxidation by permanganate. 3. Block of water quality assessment according to the content of specific substances having toxic and radiation effects. This group includes water quality indicators for total iron, aluminum and fluoride content. The definition of sub-categories of water quality was determined according to the average values of group and block indices. The same methodology helped to assign certain classes and categories to environmental conditions: class I with one category (1) – excellent; class II – good, with two categories: very good (2) and good (3); class III – satisfactory, with two categories: satisfactory (4) and mediocre (5); class IV with one category (6) – bad; class V with one category (7) – very bad [ROMANENKO, ZHUKINSKIY 1998].

The research provided phytoindication of the ecological regime of *U. australis* growth sites according to Tsyganov's ecological scales [TSYGANOV 1983].

Due to the fact that aquatic phytocenoses are dynamic and sensitive to anthropogenic pressure the current study performed a complex of calculations that mathematically interpreted the species diversity of these geosystems data: species richness (Margalef's index), species evenness (Pielou's index), a dominance index (Simpson's index), a diversity index (Shannon's index) [BEGON *et al.* 1986].

The Margalef's species richness index (d) was determined by the Equation (1) [MARGALEF 1969]:

$$d = \frac{S-1}{\ln N} \quad (1)$$

Where: S = the number of species, N = the number of individuals.

The Simpson's dominance index (c) was determined by the Equation (2) [SIMPSON 1949]:

$$c = \sum \left(\frac{n_i}{N} \right)^2 \quad (2)$$

Where n_i = the assessment of the importance of each species (quantity, biomass, etc.); N = the sum of the significance assessments.

The total Shannon's diversity (H_S) was calculated by the Equation (3) [SHANNON 1948]:

$$H_S = - \sum_{i=1}^S \left(\frac{n_i}{N} \right) \ln \left(\frac{n_i}{N} \right) \quad (3)$$

Where: n_i = the number of individuals of the species i ; N = the total number of individuals; S = the number of species.

The Pielou's evenness index (E) was determined by the Equation (4) [PIELOU 1975]:

$$E = \frac{H}{\log S} \quad (4)$$

Where: H = the Shannon's index; S = the number of species.

Statistical data processing was carried out in accordance with generally accepted methods [PEARCE 1983] using software Statistica 12.

RESULTS AND DISCUSSION

DISTRIBUTION OF *UTRICULARIA AUSTRALIS* AND ITS PARTICIPATION IN WATER CENOSES IN UKRAINE

In Ukraine, *U. australis* was first reported by Dubliany near Lviv (after Knapp, as *U. neglecta* Lehm.), listed in the "Flora of the Ukrainian SSR" [VISIULINA 1961]. This indi-

cation was probably incorrect, as well as the indication of *U. neglecta* for the suburbs of Kyiv. In fact, both localities were mentioned only in the old literature but not confirmed by herbarium collections; in addition, there is a high probability that it was *Utricularia vulgaris* and then the species was not identified correctly. The first herbarium collection of the species in Ukraine was carried out in the Transcarpathia area in 1997, and further in this region, numerous species sites were found in Mukachiv, Berehiv and Uzhgorod districts [PROTS 2009] – Figure 1.

In 2006, *U. australis* was found by DANYLYK *et al.* [2007] in Kosiv, Ivano-Frankivsk region, where the species grew up in the salt Lake Banske on the site of a former salt mine, near the shore, on the territory of the “Hutsulshchyna” National Nature Park.

In Ukrainian Polissia (northern part of Ukraine), *U. australis* firstly was collected in 2012 by IAKUSHENKO and ORLOV [2015]. In following few years, 12 localities of the species were already known in this region [DUBOVİK *et al.* 2016]. In 2019, 16 localities of *U. australis* were known in Ukrainian Polissia [ORLOV 2019]. Since the number of *U. australis* specimen has been rapidly growing over the past 10 years and the number of *U. vulgaris* specimen has been decreasing, a hypothesis has been put forward about the competitive relationship between *U. australis* and *U. vulgaris* in the region and the displacement of the latter species from suitable biotopes [DUBOVİK *et al.* 2016].

Currently, 29 *U. australis* localities are well known in Ukraine. Their current geographical distribution and descriptions of their structure are given in Table 2.

The localities of the species in Ukraine were distributed according to biotopes as shown below (Fig. 2).

Data in Figure 2 indicate that cenoses with *U. australis* were found in both natural and artificial reservoirs. Artificial biotopes prevail among the localities – 22 (75.9% of the total number of localities), of which 9 are ponds, 4 quarries, 4 drainage channels, etc.

The species was recorded in natural biotopes – oxbows – 5 localities and lakes – 2 localities (24.1% of all localities).

Pilot studies have shown that in Ukrainian Polissia *U. australis* forms free-floating pleustonic communities typical for aquatic bladderworts, but it also occurs as an aggregation in the complex of littoral vegetation. In our previous investigation, four floristic associations with participation of *U. australis* were distinguished [IAKUSHENKO, ORLOV 2015]: *Nitelletum mucronatae* Corillion et Guerlesquin 1972; *Equiseto fluviatilis-Caricetum rostratae* Zumpfe 1929 (syn. *Carietum rostratae* Rübél 1912); *Equisetetum fluviatilis* Nowiński 1930 and *Utricularietum australis* Müller & Görs 1960.

The accumulation of geobotanical data has provided more complete information to classify and characterize cenoses with the participation of *U. australis*. According to the generalization of 46 geobotanical relevés (Tab. 1), a corresponding syntaxonomic scheme was made:

- Lemnetea O. de Bolòs et Masclans 1955**
- Lemnetalia minoris* O. de Bolòs et Masclans 1955
- Utricularion vulgaris* Passarge 1964
- Utricularietum australis* T. Müller et Görs 1960

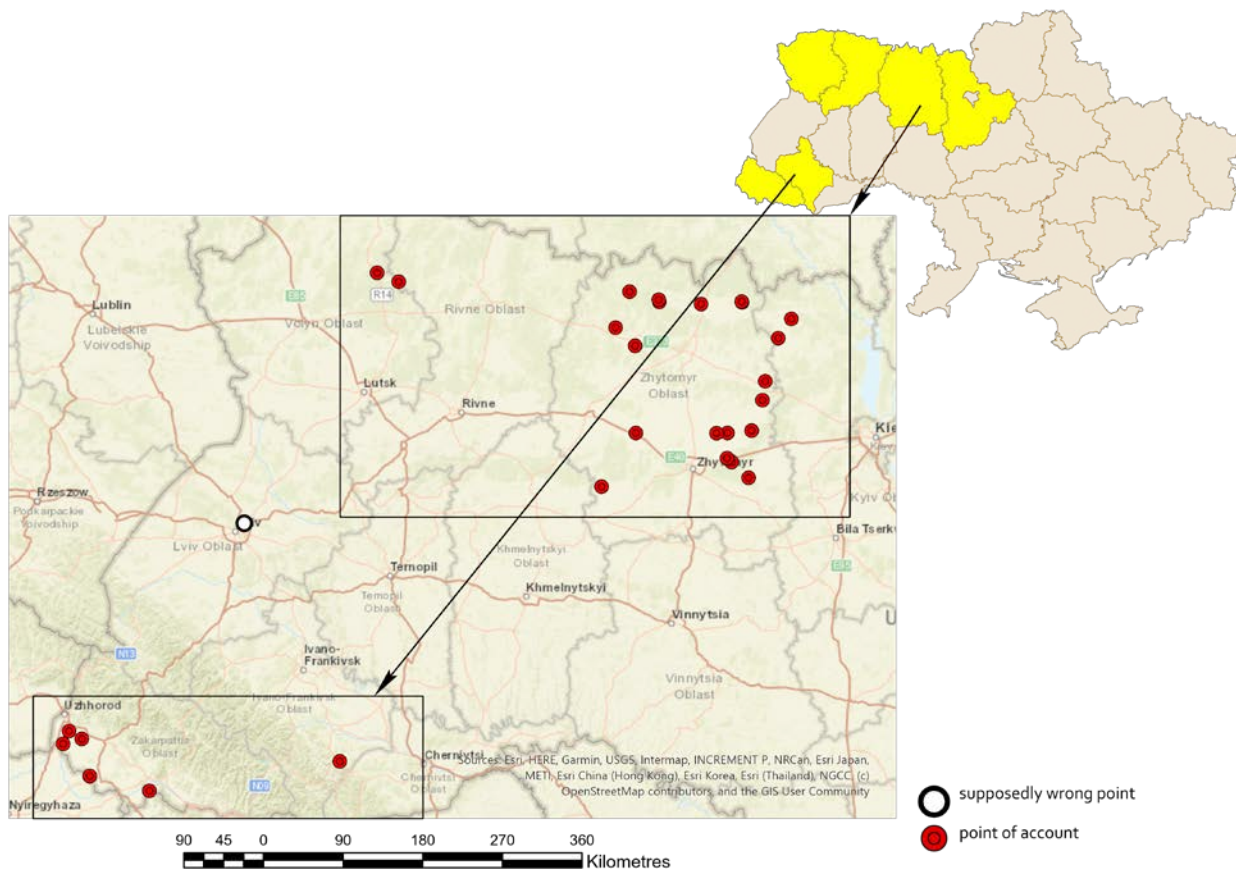


Fig. 1. Modern distribution of *Utricularia australis* in Ukraine; source: own study

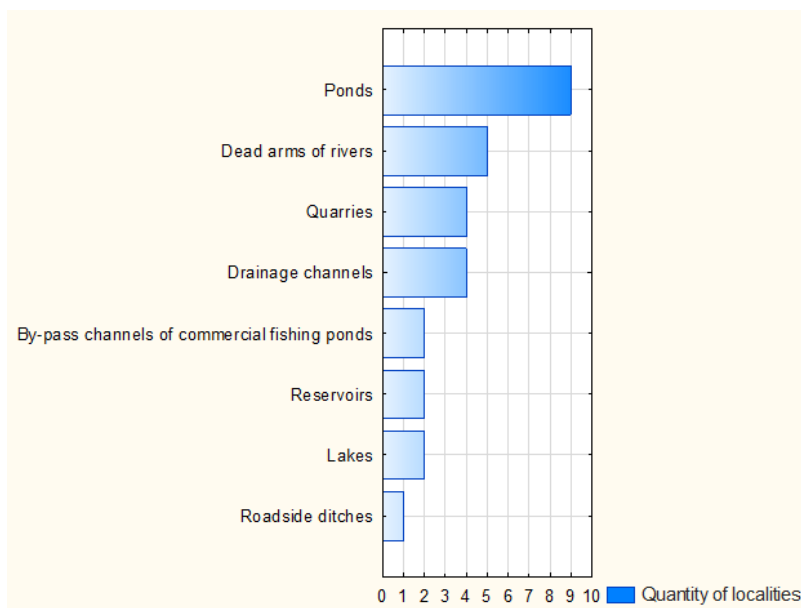


Fig. 2. Distribution of *U. australis* localities in Ukraine on biotopes; source: own study

Stratiation Den Hartog et Segal 1964

Hydrocharito-Stratietum aloidis (van Langendonck 1935) Westhoff in Westhoff et Den Held 1969

***Charetea intermediae* F. Fukarek 1961**

Charetalia intermediae Sauer 1937

Charion intermediae Sauer 1937

Charetum globularis Zutshi ex Šumberová, Hrivnák, Rydlo et Ořahel'ová in Chytrý 2011

Nitelletalia W. Krause 1969

Nitellion flexilis W. Krause 1969

Nitelletum mucronatae Tomaszewicz ex Hrivnák et al. 2001

***Littorelletea uniflorae* Br.-Bl. et Tx. ex Westhoff et al. 1946**

Littorelletalia uniflorae Koch ex Tx. 1937

Littorellion uniflorae Koch ex Klika 1935

Ranunculo-Juncetum bulbosi Oberd. 1957

***Phragmito-Magnocaricetea* Klika in Klika et Novák 1941**

Phragmitetalia Koch 1926

Phragmition communis Koch 1926

Phragmitetum australis Savič 1926

Equisetetum fluviatilis Nowiński 1930

Typhetum angustifoliae Pignatti 1953

Magnocaricetalia Pignatti 1953

Magnocaricion gracilis Géhu 1961

Caricetum ripariae Máthé et Kovács 1959

Magnocaricion elatae Koch 1926

Equiseto fluviatilis-Caricetum rostratae Zumpfe 1929

Oenanthetalia aquatica Hejný ex Balátová-Tuláčková et al. 1993

Eleocharito palustris-Sagittarion sagittifoliae Passarge 1964

Oenanthetum aquatica Soó ex Neuhäusl 1959

In general, *U. australis* in Ukraine forms its own association of a high coverage. It also occurs in other aquatic

vegetation cenoses. In addition, this species is noted in various cenoses of coastal-aquatic vegetation.

Utricularietum australis is the most widespread association in Ukraine from the *Lemnetea* class where *U. australis* grows. It develops under light exposure in natural and artificial eutrophic reservoirs, characterized by standing or slowly flowing waters with a reaction of water close to neutral. These reservoirs were 30–190 cm deep and have sandy, silt-sandy or silt bottoms. The number of species in the association is low, ranging from only 1 species – *U. australis* with a coverage of 50–60% (relevé No. 4) to 8 species (relevés No. 9, 34). The layer above water with coverage of 10–15% is formed by species such as *Hydrocharis morsus-ranae* L. – 3–5%, *Spirodella polyrhiza* L. – 1–3%, *Lemna minor* L. – 3%. The underwater layer was characterized by the coverage of 40–60%, dominated by *U. australis* – 35–40%, with significant participation of *Ceratophyllum submersum* L. – 5%, *Lemna trisulca* L. – 3%. In the syntaxonomical scheme above, no groups of *Potamogetonetea* class was found because this research used phytosociological relevés where the cover of species, such as *Nuphar lutea* L., *Potamogeton natans* L., *Myriophyllum spicatum* L. was much less than the covered vegetation area of *U. australis*, so they all were classified as *Utricularietum australis* (e.g. relevé No. 8). The cover of the underwater layer was 60–70%. It was dominated by *U. australis* – 30–45%, with significant participation of *Ceratophyllum submersum* – 10–20%. Under these phytocenotic conditions, the depth of the eutrophic reservoir reached 190 cm, water was slowly flowing, and the bottom was with a 25–30 cm layer of silt and the number of species was 8. The coverage of abovementioned layer was 45–55%. Significant participation in the formation of this layer is taken by: *Nuphar lutea* – 15%, *Trapa natans* – 5–10%, *Hydrocharis morsus-ranae* – 5–10%, *Lemna minor* – 5%, *Spirodella polyrhiza* – 5%.

The current study predicts that with the accumulation of phytocenotic data in the study area, water cenoses of

Potamogetonetea which includes *U. australis*, may be identified in the future.

Also the association of *Hydrocharito-Stratiotetum aloidis* was found in class *Lemnetea* in Ukraine (relevés No. 7 and 12). Relevé No. 7 was made in a closed non-flowing oxbow in the floodplain of the Uzh River, characterized by stagnant water and full light exposure. The water depth reached 70 cm, the bottom had a silt layer of 30–40 cm. There were 11 species in the phytocenosis. The coverage of the abovewater layer reached 75–80%, and it was dominated by *Stratiotes aloides* L. – 60%, with number of *Hydrocharis morsus-ranae* – 5%, *Lemna minor* – 1–3%. The coverage of the underwater layer reached 60%, its basis was formed by *U. australis* 35–40% with significant number of *Elodea canadensis* – 15% and *Lemna trisulca* – 10%.

In Transcarpathia, the abovementioned association was widespread in drainage channels (relevé No. 12), with full light exposure and a very slow flow. The water depth reached 70–80 cm, the bottom had a silt layer of 30–45 cm. There were 7 species in the phytocenosis. The coverage the abovewater layer reached 80–95%, and it was dominated by *Stratiotes aloides* – 80–85% and significant number of *Hydrocharis morsus-ranae* – 3%, *Lemna minor* – 5%. In the underwater layer, with the projective coverage of 30–35%, grow *Ceratophyllum demersum* L. – 20% and *U. australis* – 5–7%. In this association, the latter species has the least projective coverage.

In the class *Charetea intermediae*, two associations were identified in the study area. *Charetum globularis* association was investigated on shores in a standing eutrophic reservoir in a clay quarry with neogene saline clays of marine origin (relevés No. 1, 2, 19–25). The water depth was 5–20 cm, the clay bottom was covered with a thin layer of silt, lighting was full, and the number of species varied from 6 to 10. According to the current study and 4-year observations, this reservoir dries up in the second half of the summer period. Although the water depth decreases to 0–1 cm, *U. australis* satisfactorily develops and blooms on wet sludge. The projective coverage of the abovewater layer reached 30–35%, with a dominance of *Agrostis stolonifera* L. – 35%, and a small part was occupied by *Lemna minor* – 1%, *Lythrum salicaria* L. and others. The underwater layer was dense, with a projective coverage of 80–90%, dominated by *U. australis* – 50–60% and *Chara globularis* Thuill. – 30–40%.

The second association from the class *Charetea intermediae* investigated in Ukraine was *Nitelletum mucronatae* (relevés No. 3, 32). It was found in small shallow eutrophic reservoirs with stagnant water near a granite quarry. The reservoirs were about 50 cm deep, the bottom was clay-silt, the silt layer was 15–20 cm. There were 15 species in the cenosis. In the abovewater layer with a coverage up to 30%, occurred *Glyceria plicata* (Fr.) Fr. – 5–10%, *Hydrocharis morsus-ranae* – 5%, *Lemna minor* – 3% and others. The coverage of the underwater layer reached 100%, and the water was filled with plants to its full depth. The aforementioned layer was dominated by *U. australis* – 40% and *Nitella mucronata* (A. Braun) F. Miquel – 35–40%. A significant coverage is characteristic for *Cera-*

tophyllum demersum – 10%, *Batrachium circinatum* (Sibth.) Spach – 5%, and *Lemna trisulca* – 1%.

Class *Littorelletea uniflorae* was represented in Ukraine by the only association with *U. australis* – *Ranunculo-Juncetum bulbosi*. It was rare in the region and had two species listed in the red data book of Ukraine – *Juncus bulbosus* L. and *U. australis* (relevé No. 37) [DIDUKH (ed.) 2009]. It was described to be present in a shallow reservoir of 5–15 cm in depth located in a sandy quarry. Its bottom was sandy, lighting was full, and the number of species was 6. In the abovewater layer, dominated *Juncus bulbosus* – 60%. This layer with a small projective coverage also included *Equisetum fluviatile* L., *Ranunculus flammula* L., and *U. australis* – 50–60% dominated in the underwater layer.

The class *Phragmito-Magnocaricetea* represents coastal-aquatic coenoses. *U. Australis*, as a part of it, was found in 6 floristic associations in Ukraine.

The association *Phragmitetum australis* has been reported to be found in the Ivano-Frankivsk region, Kosiv district, Kosiv, the Lake Banske (relevé No 41). The reservoir was eutrophic and saline because it was formed as a result of the collapse of an old salt mine. The water depth was 80 cm and lighting was full. The cenosis was coastal, and the projective coverage of the abovewater layer reached 70%. It was formed by *Phragmites australis* (Cav.) Trin. ex Steud. The projective coverage of the underwater layer was 55–60%, with dominating *U. australis* – 50%. *Lemna trisulca* – 5% also occurred in the layer.

The same reservoir on the shore also contained the association *Typhetum angustifoliae* (relevé No 10). The water depth ranged from 40–60 cm and lighting was full. The abovewater layer was thick, even, with a projective coverage of about 80%. It was dominated by *Typha angustifolia* L. – 80%. The projective coverage of the underwater layer reached 45–50%. It was dominated *U. australis* – 35–40%.

The association *Equisetum fluviatilis* has been found in a pond (relevé No 33), in a 4–5 m wide coastal strip. The meso-eutrophic reservoir is 40–50 cm deep with a sandy-silt bottom and a 15–20 cm layer of silt. Shading from the trees is provided in the first half of the day. The projective coverage of the above water layer is 55–60%. *Equisetum fluviatile* (50%) dominates the area, *Carex rostrata* Stokes (5%) occurs with high frequency. The projective coverage of the underwater layer ranges from 35 to 40%. The layer is dominated by *U. australis* (35–40%).

In the other part of the same reservoir, the association *Equiseto fluviatilis-Caricetum rostratae* (relevé No. 6) has been found. The water depth is 60–80 cm, the bottom is silt, the silt layer was 15–20 cm, and the number of species is 11. The projective coverage of the above water layer was 45–50%. It is dominated by *Carex rostrata* (35%), less often occur *Equisetum fluviatile* (5%). The underwater layer has a projective coverage about 50%, and it is created by *U. australis* (about 50%).

The association of *Caricetum ripariae* Máthé et Kovács 1959 has been investigated in a forest lake where it forms a broad (2–4 m) shoreline (relevé No. 14). The 30–50 cm deep reservoir is eutrophic with a silty bottom and a 15–20 cm silt layer. Shading from the trees is provided in

the first half of the day. The projective coverage of the above-water layer is 55–60%. It is dominated by *Carex riparia* Curtis (45%), whereas less involved in the formation of this layer are *Hydrocharis morsus-ranae* (5%), *Lythrum salicaria* (3%), *Lemna minor* (1%). The projective coverage of the underwater layer is 40–50% formed by *U. australis*.

The *Oenanthe aquatica* association has been investigated in a eutrophic reservoir in a clay quarry near the shore (relevé No 26). The reservoir is 10–20 cm deep with a clay bottom, and full lighting. The above-water layer has been thin, with a projective coverage of 15–20%. It consisted of *Oenanthe aquatica* (L.) Poir. (10%), *Eleocharis palustris* L. (5%), and *Lemna minor* (1%). The underwater layer has a projective coverage of 50–55%, dominated by *U. australis* (40–50%).

In Europe in general, *U. australis* is a rare species inlisted with the LC category (least concern) into the European Red List of Vascular Plants [BILZ *et al.* 2011] and the IUCN Red List of Threatened Species [CHAMPION 2014]. In addition, its habitats are protected according to Resolution 4 of the Bern Convention [EVANS, ROEKAERTS 2015]: C1.224 Floating *Utricularia australis* and *Utricularia vulgaris* colonies – free-floating communities of more or less nutrient-rich Palaeartic waters dominated by bladderworts (*Utricularia australis*, *Utricularia vulgaris*) in plant communities *Hydrocharition: Lemno-Utricularietum vulgaris*, *Utricularietum australis* (*Utricularietum neglectae*). In Ukraine, *U. australis* is inlisted into the Red Data Book of Ukraine as a vulnerable species [PROTS 2009].

THE INVESTIGATION OF ECOLOGICAL FEATURES OF PHYTOCENOSES WITH THE PARTICIPATION OF *UTRICULARIA AUSTRALIS*

There are multiple proofs of global warming for the groups of hydrobionts. Thus, we increasingly often observe a shift in seasonal phenomena, such as heat stress, negative influence on the growth and development of native species, change of the ratio of native species, move of the species from warmer regions to the north, restructuring of species, and structure and character of the functioning of ecosystems. All this disrupts the stability of aquatic ecosystems [The Royal Society 2010]. Under these conditions, favourable conditions are created for the spread of species with a wider range of temperature tolerance. On the Tsyganov's thermoclimatic scale, *U. australis* has a fairly wide range of geographical distribution – from the subarctic to the sub-Mediterranean (3–11). Therefore, the territory of Ukraine, belonging to the subboreal type, is favourable for the distribution of the species (Fig. 3). *U. australis* has a wider range on the continental scale of climate – from oceanic type of the 2nd ocean ecological suite with point 3 to ultra-continental with point 12. According to the Tsyganov's cryoclimatic scale, *U. australis* can withstand the regime from very cold winters of the 1st hypercryothermal ecological suite to warm winters of the acryothermal ecological suite (1–11 points). Thus, the climatic conditions of Ukraine are quite favourable for the spread and formation of phytocenoses with the participation of *U. australis*.

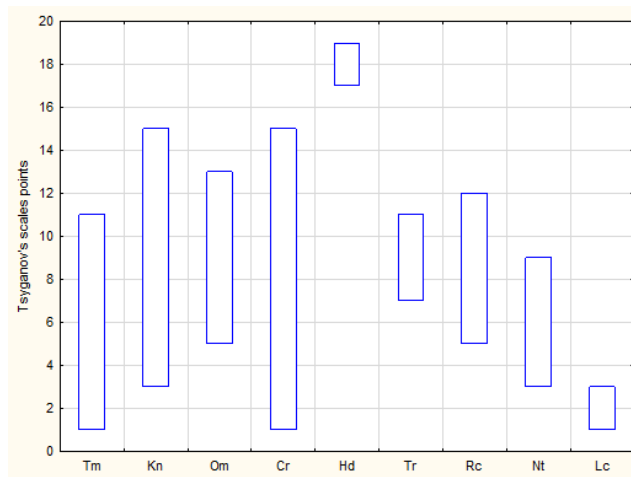


Fig. 3. Tolerance range of *Utricularia australis* according to Tsyganov's scale; Tm = thermoclimatic scale (number of gradations – 17); Kn = scale of continental climate (number of gradations – 15); Om = ombroclimatic aridity-humidity scale (number of gradations – 15); Cr = cryoclimatic scale (number of gradations – 15); Hd = humidity scale (number of gradations – 23); Tr = scale of salt regime (number of gradations – 19); Nt = scale of nitrogen enrichment (number of gradations – 11); Rc = scale of acidity (number of gradations – 13); Lc = scale of luminance-shading (number of gradations – 9); source: own study

It should be noted that according to the Tsyganov's scale, the narrowest endurance regime of *U. australis* is marked on the soil moisture scale – from a marsh-forested type of a marsh-forested ecological suite (17 points) to a marsh type of a marsh ecological suite (19 points). In our research, the wetting conditions have a wider variation than shown by the Tsyganov's scale – from deep-sea ecosystems to drying shallow water bodies. In the latter, *U. australis* transforms into a surviving form.

On the scale of luminance-shading (Lc), *U. australis* has a narrow tolerance range – from open spaces of extra-forestral (light) ecological suite to semi-open spaces of shrub ecological suite (range – 1–3). However, another study indicates a much wider range of shade tolerance (from very shady conditions ($64 \mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, Pat 2) to full incident light exposure ($>2600 \mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, Dec 2) [CESCHIN *et al.* 2020]).

The previous study noted the dependence of different indicators on water quality due to aquatic plants [FEDONIUK *et al.* 2019; FEDONYUK *et al.* 2020; ROMANCHUK *et al.* 2018]. However results from other studies showed that there were no dependencies between the diversitological indices of phytocenoses with the participation of *U. australis* and the water colour, as well as the common iron content, which, along with the content of the suspended particles, determines the water coloration. In this study, the indicator shows a wide range of variations – from 11 to 134 degrees, which is due to the nature of the soil cover in the water basin, the presence of humus substances in water, as well as the chemical composition of groundwater and its increased role in the nutrition of rivers in the region (Fig. 4). Increased concentrations of common iron in rivers of Ukrainian Polissia are due to geochemical processes, since in these river basins, groundwater with the highest concen-

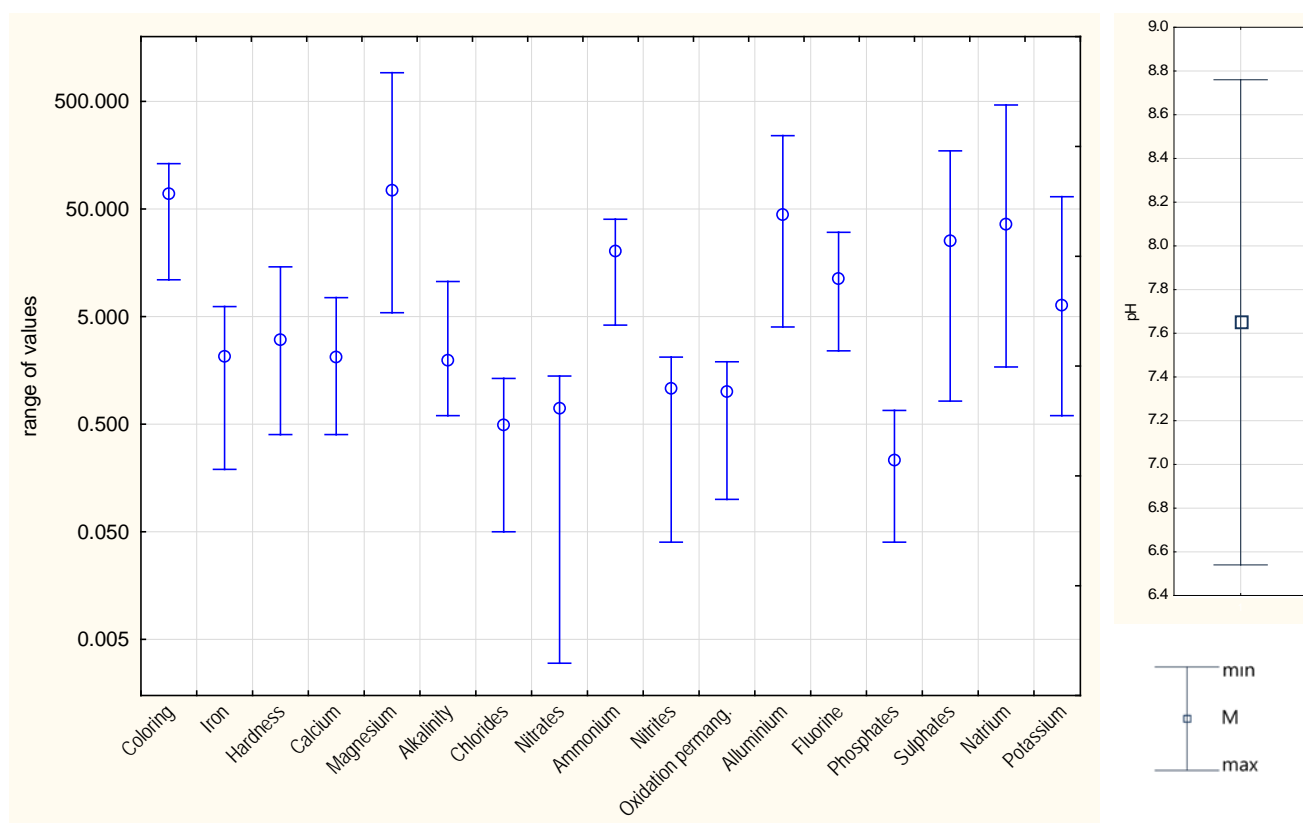


Fig. 4. Physical and chemical water parameters in the investigated sites of *Utricularia australis* in Ukraine; source: own study

tration of iron ions in Ukraine of up to $8 \mu\text{g}\cdot\text{dm}^{-3}$ is discharged [FEDONIUK *et al.* 2019]. Such conditions determine the distribution of species that are able to survive in conditions of high concentration of common iron in the water, which translates into its strong coloration in various shades of brown.

Figure 4 shows that the hydrochemical parameters of water at the growth sites of *U. australis* in Ukraine are significantly different from the published data for Poland [OCHYRA 1985], Slovakia [OĀHAĀELOVÁ 1980] and Hungary [KÁRPÁTI 1963]. In particular, all localities of the species in Ukraine are found in eutrophic reservoirs. In no case has the species been found in reservoir inside oligotrophic or mesotrophic swamps, as well as in oligotrophic or mesotrophic ponds.

The results of the statistical processing show that hydrochemical parameters of the species in Ukraine have such range: pH from 6.54 to 8.76. The average for 18 localities is 7.3 ± 0.40 (Fig. 4). The given range of water acidity covers most of the data provided by researchers for various regions of Europe [ADAMEC 2008; CESCHIN *et al.* 2020; RODRIGO, CALERO 2019; SIROVÁ *et al.* 2014], but it is lower than on transition peat bogs [OCHYRA 1985], oligotrophic or mesotrophic hollows in peat bogs [SPAŁEK 2006] in Poland.

In the habitats of *U. australis*, the nitrates content was $0.6\text{--}10.6 \text{ mg}\cdot\text{dm}^{-3}$ ($1.96 \pm 0.564 \text{ mg}\cdot\text{dm}^{-3}$) and ammonium – $< 0.05\text{--}1.33 \text{ mg}\cdot\text{dm}^{-3}$ ($0.49 \pm 0.087 \text{ mg}\cdot\text{dm}^{-3}$). The excess of nitrate content over the ammonium form of nitrogen was given by researchers earlier for Lower Silesia, Poland [KOSIBA 2004], but it was opposite comparing with

the results for Třeboň basin [ADAMEC 2008] and Trebonsko Biosphere Reserve, South Bohemia, Czech Republic [SIROVÁ *et al.* 2014], where the predominance of NH_4^+ among nitrogen forms over the nitrate form was observed. The average nitrate concentration in water was close to the values given for Central Italy ($800\text{--}1600 \mu\text{g}\cdot\text{dm}^{-3}$) [CESCHIN *et al.* 2020].

The range of calcium content in the water of the associations studied turned out to be very wide – $4.0\text{--}240.5 \text{ mg}\cdot\text{dm}^{-3}$ ($44.31 \pm 12.693 \text{ mg}\cdot\text{dm}^{-3}$), close to the one published by KOSIBA [2004]. However, it was significantly higher than cited by ADAMEC [2008]. The average potassium content found by the study was $6.37 \pm 3.52 \text{ mg}\cdot\text{dm}^{-3}$, which was higher in comparison with data obtained in Poland [ADAMEC 2008; KOSIBA 2004]. The ranges of the content of other important ions in the water of the habitats of *U. australis* in Ukraine were as follows: Na – $1.7\text{--}173.8 \text{ mg}\cdot\text{dm}^{-3}$ ($36.11 \pm 25.238 \text{ mg}\cdot\text{dm}^{-3}$); chlorides – $5.43\text{--}923.2 \text{ mg}\cdot\text{dm}^{-3}$ ($74.65 \pm 50.039 \text{ mg}\cdot\text{dm}^{-3}$); and sulphates – $0.82\text{--}173.8 \text{ mg}\cdot\text{dm}^{-3}$ ($25.26 \pm 12.472 \text{ mg}\cdot\text{dm}^{-3}$). Of all the ions we studied, the lowest concentrations of *U. australis* cenoses in water were characteristic for phosphorus, which corresponds to the data of other researchers [CESCHIN *et al.* 2020].

According to the water acidity scale, *U. australis* has a wide tolerance range – from weakly acidic waters of the mesoacidophilic 1st ecological suite (5 points) to the intermediate one between alkaline and alkaline waters of a mesoalkylphilic ecological suite (12 points). As the species grows in waters of different acidity, changes in different parameters are revealed. In our research *U. australis*

was observed in reservoirs with a pH range from 6.54 to 8.76, or from category 1 quality class I (excellent) to category 7 quality class V (very bad). In this range, no changes in the vitality of *U. australis* were recorded; it developed equally well in both acidified and alkaline aqueous solutions. According to these data, a weak direct correlation was observed between the coverage of *U. australis*, the Shannon's index and the Pielou's evenness index. The calculated Shannon–Wiener index and their comparison with the acidity of *U. australis* water showed the lack of reliable relationships in the variation of the species projective coverage, which testifies to the ability of the species to spread over a wider range than indicated by the Tsyganov's ecological scale (Fig. 3).

It is obvious that indices of generalized biodiversity and species richness decrease in inverse proportion to the intensity of anthropogenic factors on biological objects [HUGHES 1978; NAGENDRA 2002]. A corresponding trend has been observed in this research. This is confirmed by the correlation coefficient we set ($r = 0.41$), which indicates a moderate direct relationship between the parameters in pH range from 4.5 (lowest value) to 7.4 (highest value) (Fig. 5).

The Pielou's evenness criterion (E) determines the magnitude of the probable fluctuation in the number of species in a population. It is an indicator of the even distribution of individual species by the number of individuals in a population. The richer species composition, biocenoses have higher environmental tolerance than numerically small ones. Therefore, the Pielou's criterion determines the degree of biocenosis stability through two main indicators – species diversity and population [ADAMEC, POPPINGA 2016]. The current study estimated a moderate direct relationship between water pH and Pielou's indices of phytocenoses with coverage of *U. australis*. This was confirmed by the coefficient of correlation ($r = 0.43$).

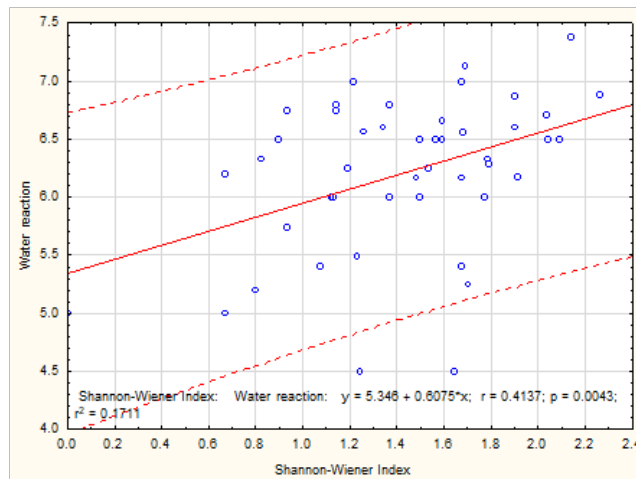


Fig. 5. Shannon–Wiener index in phytocenoses with *Utricularia australis* at different pH levels of water; source: own study

According to the Tsyganov's salt regime scale, the endurance range of *U. australis* was insignificant – from sufficiently rich waters of the glycosemiotrophic ecological suite to slightly saline waters of the haloetvrophic ecological suite (7–11 points).

The current study analysed a number of indicators related to the content of salts in water and their relation to the structure of the phytocenoses (Tab. 3, 4). The water hardness in observation points ranged from 0.4 to 14.5 $\text{mmol}\cdot\text{dm}^{-3}$. Close correlations were found between this index and all other indicators except the Margalef's index. The water hardness and the Shannon's and Pielou's indices were moderately close ($r = 0.45$ for both indicators), and the Simpson's dominance indices ($r = -0.71$) very close. This indicated that with the increase of water hardness, the dominance of *U. australis* decreases. The established dependencies were fully consistent with other data on water

Table 3. Different indicators of phytocenoses with participation of *Utricularia australis*

Relevé	Abovewater layer			Underwater layer			
	D	H	E	d	$C_{U. australis}$	H	E
1	1.9276	0.3260	0.5415	0.5117	1.4472	0.6365	2.1145
2	2.4802	0.9584	1.3712	0.5117	1.3856	0.6682	2.2199
3	4.0620	1.7046	2.0170	3.5000	1.1210	1.5057	1.6672
4	1.9205	1.0671	2.2365	1.1896	1.6180	0.5608	1.1754
5	3.3743	1.4365	1.6998	2.8119	1.2533	1.4735	1.8936
6	4.8391	1.1815	1.2381	0.5856	1.7550	0.0965	0.3206
7	4.2037	1.1153	1.1688	1.1248	1.3537	0.9596	2.0113
8	2.2984	1.4143	2.0234	1.1248	1.2533	1.0114	2.1198
9	3.8410	1.4990	2.1446	1.1248	1.4472	0.8676	1.8183
10	0.5240	0.0665	0.2210	1.2098	1.5632	0.6655	1.3947
11	1.4307	0.9503	1.9917	3.1999	0.9153	1.7839	2.1108
12	1.5000	0.5793	0.9622	1.3288	0.8290	0.9163	1.9204
13	3.0745	1.0456	1.4959	1.0840	1.4980	0.7589	1.5907
14	2.8730	0.7594	0.9759	–	1.7725	–	–
15	3.3850	1.6441	2.1128	2.2495	1.2533	1.3580	1.9428
16	4.1201	1.7632	1.9524	0.5886	1.5853	0.5004	1.6623
17	3.3096	1.1726	1.3875	1.1248	1.6180	0.6576	1.3783
18	3.0244	1.0389	1.3350	2.0732	1.2159	1.3854	1.9820

Explanations: d = the Margalef's index, H = the Shannon's index, E – the Pielou's index, $C_{U. australis}$ = the Simpson's dominance index for *Utricularia australis*.

Source: own study.

Table 4. Correlation between water quality and diversitological indicators of phytocenoses with the participation of *Utricularia australis*

Variable	Correlation coefficient for			
	<i>d</i>	<i>H</i>	<i>E</i>	<i>C_{U. australis}</i>
Colour (degree)	0.2698	-0.0074	-0.5952	0.2270
pH	-0.1151	0.0072	0.4356	-0.0443
Fe common (mg·dm ⁻³)	0.0467	-0.0972	-0.3365	0.3244
Hardness common (mmol·dm ⁻³)	0.3249	0.4485	0.4515	-0.7107
Calcium (mg·dm ⁻³)	0.2566	0.3556	0.3820	-0.6552
Magnesium (mg·dm ⁻³)	0.2255	0.3519	0.3946	-0.4287
Alkalinity common (mmol·dm ⁻³)	0.6679	0.7675	0.5461	-0.6810
Chlorides (mg·dm ⁻³)	0.2673	0.4453	0.6741	-0.6323
Nitrates (mg N·dm ⁻³)	0.1863	0.3224	0.3214	-0.7016
Ammonium (mg N·dm ⁻³)	-0.0568	-0.2617	-0.6488	0.2649
Nitrites (mg N·dm ⁻³)	0.2265	-0.0605	-0.6422	0.4192
Oxidation permanganate (mg O ₂ ·dm ⁻³)	-0.2995	-0.5219	-0.8236	0.6027
Aluminium (mg·dm ⁻³)	0.0505	0.1535	0.1881	-0.3407
Fluorine (mg·dm ⁻³)	0.3802	0.2753	0.1173	-0.0519
Phosphates (mg·dm ⁻³)	0.3497	0.3886	0.0416	-0.2403
Sulphates (mg·dm ⁻³)	0.0209	0.1167	0.2306	-0.6717
Sodium (mg·dm ⁻³)	0.1282	0.2325	0.4919	-0.2918
Potassium (mg·dm ⁻³)	-0.1149	0.0201	0.3632	-0.4831

Explanations: *d*, *H*, *E*, *C_{U. australis}* as in Table 2; marked correlations are significant at $p < 0.05$.

Source: own study.

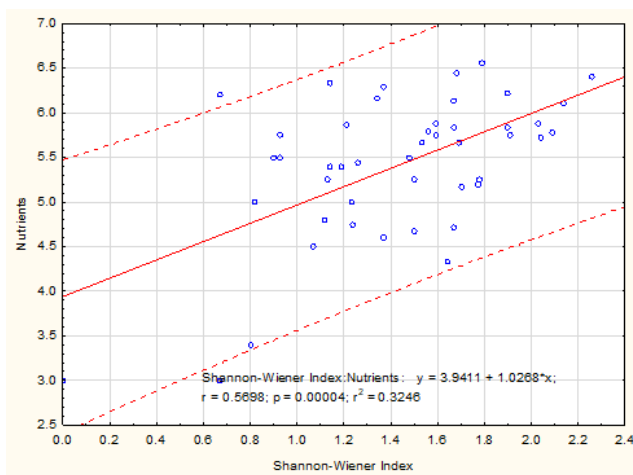


Fig. 6. Development of phytocenoses with *Utricularia australis* at different levels of nitrogen content in water; source: own study

quality and their impact on species redistribution in phytocenoses (Fig. 6).

Water common hardness was an indicator for the presence of mainly dissolved calcium and magnesium salts. Therefore, similar dependencies were noted between diversitological indices (except for the Margalef's indices) and the content of these two substances in water. The suppression of *U. australis* species occurs with the increase of calcium cations in water, with close correlation dependencies ($r = -0.66$). In terms of density, moderate direct and inverse relationships were observed between diversitological parameters and magnesium cation content ($r = 0.35-0.43$).

The content of calcium carbonate in water determines the alkalinity of water. This indicator showed close correlation with all diversitological indicators ($r = 0.54-0.77$).

Some information sources show better growth of *U. australis* on substrates richer in nitrogen [CESCHIN *et*

al. 2020], and the study has shown a directly proportional dependence of the growth of *U. australis* biomass depending on the nitrogen concentration in water [ADAMEC 2008; ADAMEC, KOVÁŘOVÁ 2006]. The current study has differentiated and investigated the influence of nitrogen forms on the growth and development of *U. australis*.

As regards the nitrogen content in water, the species has a wide range of tolerance: from very poor in nitrogen – of the 2nd subnitrophilic ecological suite (3 points) to rich in nitrogen – of the 2nd nitrophilic group (10 points).

It is known that ammonium ions form during biochemical transformations and are oxidized by the action of nitrite bacteria in nitrite ions (with subsequent formation of nitric acid) [OSYPENKO, YEVTUKH 2018]. Therefore, the analysis of nitrogen metabolism parameters was carried out in combination with the possible transformation of nitrogen content forms. The current study analysed the impact of three groups of ions: ammonium cations, and nitrate and nitrite anions. The dynamics of the concentration of ammonium cations in the studied reservoirs ranged from 0.05 to 1.33 mg N·dm⁻³ (i.e. from category 1 class I of water quality “very good” to category 6 class IV “bad” and “dirty”). The analysis of the dynamics of diversitological parameters showed that with increasing content of ammonium ions, the phytocenosis evenness was significantly reduced ($r = -0.65$).

In the localities of the *U. australis*, the content of nitrites in water vary from 0.0027 to 1.4 mg N·dm⁻³, i.e. from category 1 class I of water quality (very pure) to category 4 quality class III (mediocre). The variation was relatively insignificant. At the same time, the study found close correlations between this indicator and different indicators, except for the Pielou's evenness indices, in the case of which inverse close correlation ($r = -0.64$) was found with the nitrite content.

The study revealed the impact of nitrate anions on different indices and dominance of *U. australis*. According to

the study, their content ranged from 0.6 to 10.6 mg N·dm⁻³, from category 4 quality class III (mediocre) to category 7 quality class V (very bad). The deterioration of water quality by the nitrate content significantly influenced the decrease in the projective coverage of *U. australis*, which was reflected in a different proportion of other species in water phytocenoses.

Water oxidation is an important indicator of water quality. It characterizes the total content of organic substances and highly oxidizable inorganic impurities (hydrogen sulphide, sulphite anions, iron compounds II, etc.). These impurities enter reservoirs due to natural processes, for example with rain and melt water, as well as the development of plant and animal organisms, erosion of drains, and the drainage of sewage [FEDONIUK *et al.* 2019; KLYMENKO *et al.* 2018].

As regards clean surface water, the dissolved oxygen concentrations vary between 2–8 mg·dm⁻³ and it is an important indicator underlying decisions on the application of certain sanitary measures [FEDONYUK *et al.* 2020]. In this study, *U. australis* successfully grew at various dissolved oxygen concentrations in water. It should be noted that similar results were obtained by other researchers previously, and dissolved oxygen concentrations in water fluctuated from 0.8 to 8 mg·dm⁻³ [CESCHIN *et al.* 2020]. However, in other information sources, a narrower range of tolerance by a given plant species to the dissolved oxygen concentration was noted [ADAMEC 2008; ADAMEC, KOVÁŘOVÁ 2006]. The appearance of oxidized forms has indicated a profound process, because the increase in oxidized forms of nitrogen due to the overall decrease in biochemical oxygen demand manifested intensive oxidation of carbon compounds. In this research, *U. australis* was observed in reservoirs with a very wide range of permanganate oxidation parameters – from 4.16 to 40.15 mg·dm⁻³, from category 2 class II “good” to category 7 quality class V “very bad”. In the aquatic ecosystems examined regarding changes in permanganate oxidation, changes in species composition have been found, in particular an increase in the participation of *U. australis* in the total projective coverage of phytocenoses. This indicates a wider range of species endurance than other species of macrophytes noted in phytocenoses. In this case, evenness of phytocenoses has been significantly reduced ($r = -0.82$) and the dominance of *U. australis* increased ($r = 0.60$). Under these conditions, an increase in the participation of *U. australis* compared with other species may be an indicator of the deterioration of the oxygen regime in water bodies. In this case, the phytocenoses were significantly reduced ($r = -0.82$) and the dominance of *U. australis* increased ($r = 0.60$).

The content of fluorides in water was determined as regards specific toxic substances and radiation. This indicator ranged from 0.18 to 2.1 mg·dm⁻³, from category 1 class I of water quality (very pure) to category 4 quality class III (mediocre). The research did not find a close correlation between the fluoride content in water and the diversitology. Obviously, this was due to the fact that in every case the concentration of fluoride in water did not fall below quality class III.

The content of phosphates in water in the ecosystems studied varied from 0.04 to 0.67 mg·dm⁻³, from category 3 class II “good” to category 7 quality class V “very bad”. Despite the low water quality according to this indicator, no deterioration in the development of phytocenoses with *U. australis* was observed, and no significant dependence of the influence of increased phosphate concentrations on different parameters was found. However, in previous studies by other authors noted sensitivity of *U. australis* to high concentrations of phosphorus, with the optimal growth regime observed not higher than 10 mg·dm⁻³ [CESCHIN *et al.* 2020]. Data from the study discussed in the article show a much wider range of successful coexistence of this species.

In these localities of *U. australis*, a wide range of variations in the sulphate content was observed – from 0.82 to 173.8 mg·dm⁻³, i.e. from category 1 class I of water quality (very pure) to category 7 quality class V “very bad”. With the deterioration of water quality due to the content of sulphates, the oppression of *U. australis* ($r = -0.67$) was observed.

CONCLUSIONS

On the territory of Ukraine, *Utricularia australis* is listed in the Red Book of Ukraine with the status of “vulnerable”. About 10 years ago, on the territory of Ukraine, the species was recorded only from the Transcarpathian region and subsequently spread to the territory of western Ukraine. Within the current study, new locations were recorded. Previously, it was described that the optimal growth of *Utricularia* was associated with sunny sites and shallow waters with low aquatic inorganic phosphorus (<10 µg·dm⁻³) but higher nitrogen (800–1600 µg·dm⁻³). In this study, a wider range of adaptations with respect to the content of organogenic elements in water has been noted. The climatic conditions of Ukraine are favourable for the spread and formation of phytocenoses with the participation of *U. australis*, especially on thermoclimatic, cryothermal and continental scales. For this reason, *U. australis* is considered to be a eurytopic species that is characterized by a wide ecological amplitude of the main hydrochemical parameters in its habitats.

In the current study, a much larger tolerance range of *Utricularia australis* was observed for some parameters of water quality, including the content of nitrogen, phosphorus, and iron compounds, colour, pH, and organic pollution. Although some previous studies noted a narrower range of species endurance when exposed to different biochemical parameters, especially to the alkalinity of the environment and the phosphorus content. In the northern and western regions of Ukraine, *Utricularia* has a much wider range of endurance.

It should be noted that a slight inhibition of *U. australis* may be caused by an increase in water hardness and, accordingly, by the content of calcium and magnesium cations, especially in the form of chlorides, sulphates and nitrates.

Its tolerance to growth in artificial or natural biotopes, in a wide range of hydrochemical parameters, including

heavily polluted reservoirs, allows to predict the further distribution of this species in Ukraine and a increasing number of its localities in the country. The current status of the species in the red data book of Ukraine from 2009 year is “vulnerable”. However, the current research has shown that the status of this species should be further reviewed.

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