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THE OCCURRENCE OF PROTECTED VERTIGINIDS *VERTIGO ANGUSTIOR* JEFFREYS, 1830 AND *V. MOULINSIANA* (DUPUY, 1849) (GASTROPODA: PULMONATA: VERTIGINIDAE) IN THE ESTUARY OF THE ODRA RIVER

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Abstract: The wetlands at the Odra estuary in the environs of the Szczecin and Kamieński lagoons were surveyed for the occurrence of vertiginids, identifying their habitats and accompanying malacofauna. In total, 22 land snail species were recorded, among them five species of *Vertigo*: *V. angustior* Jeffreys (5 localities), *V. moulinsiana* (Dupuy) (3), *V. antivertigo* (Draparnaud) (15), *V. pygmaea* (Draparnaud) (20) and *V. substriata* (Jeffreys) (2). The localities of the protected *V. angustior* and *V. moulinsiana* were situated along the Dziwna Strait and the Kamieński Lagoon. In the Odra estuary, *V. angustior* and *V. moulinsiana* occurred in four plant communities: sedge beds *Caricetum gracilis*, *Caricetum distichae, Caricetum acutiformis* and herbs of the *Lysimachio-Filipenduletum* association. The inventory showed that the protected vertiginids could inhabit a landscape altered by human activities if the surrounding areas ensured constant humidity. On the contrary, intensive agricultural activities on the polders surrounding the Szczecin Lagoon excluded their occurrence. The passive transport of snails by backwater current in the Kamieński Lagoon from the abundant populations in the Karpinek Bay (both species present) may account for the distribution of vertiginids in the study area.

Key words: land snails, vertiginids, habitat, wetlands

INTRODUCTION

The European Union, joined by Poland in 2004, induced an extensive interest in ecology, conservation and management of minute species of wetland land snails of the family Vertiginidae, the narrow-mouthed whorl snail *Vertigo angustior* Jeffreys, 1830 and Desmoulin's whorl snail *V. moulinsiana* (Dupuy, 1849) among them. These species are protected under Annex II of the Habitats and Species Directive, requiring Natura 2000 sites to be designated for their protection in the member states where they occur.

V. moulinsiana was classified as critically endangered (CR in the Polish Red Data Book) and *V. angustior* as endangered (EN), because they were recorded strictly locally and the number of their populations decreased as a result of habitat destruction (Pokryszko 1990a, 2004a, b). Recently, owing to new field inventories in formerly neglected habitats such as rich fens, marshes and riparian margins, the knowledge of vertiginid distribution in this part of Europe has improved significantly (e.g. Horsák &

Hajek 2005, Zając & Zając 2006, Książkiewicz 2009, Książkiewicz et al. 2015). Several studies have also been published on the ecology of protected vertiginids in Central Europe (Horsák & Hajek 2005, Lipińska et al. 2011, Jankowiak & Bernard 2013, Książkiewicz et al. 2013) and on their life cycles (Myzyk 2011).

In spite of that, still little is known about the occurrence of those snails in some parts of Poland, including the Odra estuary, with its vast wetlands along the river banks which may be potentially attractive to vertiginids. The wetlands hold diverse habitats and have been altered by human activity to varying degrees (i.a. Jasnowski 1962, Staszewski et al. 1997, Ziarnek 1997). To date, no studies have been published on the terrestrial malacofauna of the area encompassing the Kamieński Lagoon and the Szczecin Lagoon. The aim of the study was a malacological inventory of Natura 2000 protected areas in the Odra estuary, with special reference to the presence of protected vertiginids, as well as their accompanying mollusc and plant species.

STUDY AREA

The studies were conducted in wetland meadows, pastures and wasteland situated near the Odra estuary within the boundaries of Natura 2000 protected areas: Site of Community Importance – Odra Estuary and Szczecin Lagoon PLH320018, and the Special Protection Areas for birds – Szczecin Lagoon PLB320009 and Kamieński Lagoon with Dziwna Strait PLB320011.

The Odra River discharges into the Szczecin Lagoon, which further transfers its waters into the Pomeranian Bay and the Baltic Sea through three straits: Świna, Dziwna and Piana. The Dziwna Strait near the town of Kamień Pomorski broadens and becomes the Kamieński Lagoon (Fig. 1). The estuary runs across plains composed of wetland sediments and swampy areas at the foot of ground-moraine uplands in the following mesoregions: Uznam and Wolin, Wkrzańska Plain, Goleniowska Plain, Gryficka Plain, and Lower Odra Valley (Borówka 2004).

The area directly adjoining the Szczecin and Kamieński lagoons was drained before World War I, as can be seen on German Messtischblatt maps of 1886–1900 (Anonymous 2009). Until 1989, the area was intensely used by agriculture, focusing primarily on hay production. When the ownership structure in Poland changed, causing the downfall of large farms, the intensity of agriculture decreased and some areas became abandoned. Today, most agricultural land is used for extensive farming. The most frequent activities include annual mowing combined with biomass removal and extensive cattle grazing. No agricultural activities take place over a part of the area. Fragments of the abandoned meadows, not exceeding 10% of their total area, are covered with scrub. A part of the area is taken up by still functioning polders separated from the waters of the lagoon by a levee and drained by a network of canals and pumping stations. Nearly the whole of the Szczecin Lagoon is surrounded by a levee, whereas around the Kamieński Lagoon the levees are present only sporadically. Drainage ditches in the meadows are cleaned periodically. The studied areas adjoin cultivated fields or dry brownfields and are separated from the water by a strip of reed beds, which is narrow in some places and wide in others.

The expanse of the studied habitats varied. The widest strip of the studied wetlands was situated in the environs of the Szczecin Lagoon; a polder on its eastern bank was 7.6 km wide (sampling sites 35–44). On the western bank of the Szczecin Lagoon the wetlands were 2 km wide and were partly drained. The minimum width of the studied area in that lo-

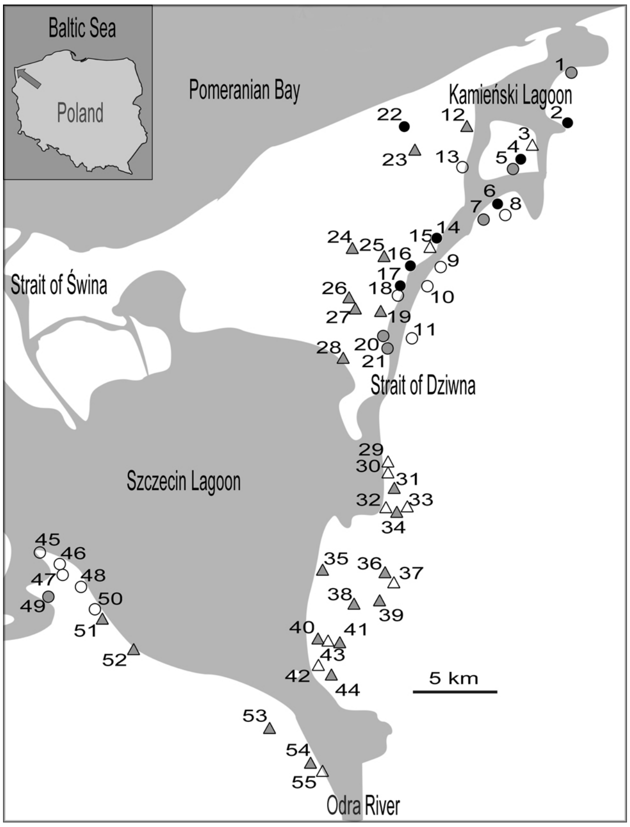

Fig. 1. Distribution of sampling sites around Szczecin Lagoon and Kamieński Lagoon. Circles indicate comparatively unaltered natural habitats and triangles indicate strongly altered habitats; no colour indicates the absence of molluscs; grey colour indicates the presence of molluscs; black colour indicates the presence of *Vertigo angustior* and/or *V. moulinsiana*

cation was 200 m. The area held habitats altered by long-lasting agricultural activities. Irregular grazing and mowing contributed to the development of meadows, where *Deschampsia caespitosa, Juncus effusus*, *Carex acutiformis*, *C. gracilis*, *Phalaris arundinacea* and *Phragmites australis* predominated. Much narrower strips of wetland surrounded the Kamieński Lagoon and the Dziwna Strait, up to 800 m wide in the widest place and merely 35 m wide in the narrowest place. A flat, damp area was found only directly beside the Strait, and farther from the water the ground was gradually rising, eventually forming a ground-moraine upland. Marshy habitats in depressions at the foot of the moraine were represented by fens with *Carex disticha*, *C. acutiformis* and *C. gracilis*, as well as patchily distributed halophytes. Moraine uplands were usually covered with meadows with *Arrhenatherum elatius*. There were no polders at the Kamieński Lagoon and the Dziwna Strait because the area was not constantly threatened with flooding; only drainage canals were present. Some of the ditches were overgrown and had become shallow due to the lack of maintenance over a period of many years.

The studies included also areas situated ca. 2 km west of the Dziwna Strait (environs of the village of Unin) and ca. 4.5 km west of the Kamieński Lagoon (near Lake Koprowo), which were also part of the wetland plain. The areas were mainly composed of degraded meadows covered with *Molinio-Arrhenatheretea* vegetation. Due to a long-term drainage and probably intensive exploitation in the past, the habitat was characterised by organic soil, strongly mineralised substrata and floristically uniform phytocoenoses with tussock grass *Deschampsia caespitosa*.

MATERIAL AND METHODS

The sampling sites were selected based on a detailed field inspection, enabling evaluation of the character of vegetation and current moisture levels of the respective habitats. Samples were collected from sites where vertiginids might potentially occur (cf. Adamski et al. 2004).

The ground moisture level was determined according to a five grade scale (Killeen & Moorkens 2003): 1 – dry (no visible moisture on ground surface); 2 – damp (ground visibly damp, but water does not rise under pressure), 3 – wet (water appears under light pressure), 4 – very wet (pools of standing water present), 5 – site under water (entire sampling site in standing or flowing water over 5 cm deep).

Samples were collected by the senior author in the vegetation season of 2012. In each site, samples were collected from three to five spots, each of the size 10 × 10 cm, in June, and then again at the end of September. Both litter and topsoil were collected, which is the recommended sampling procedure for *V. angustior* (Książkiewicz et al. 2012). Succineids and large snails were collected by hand. In the laboratory, the samples were dried and passed through sieves with 5, 2, 1 and 0.5 mm mesh. Each fraction was examined for molluscs under a stereomicroscope.

Vertiginids were identified according to Pokryszko (1990a) and the other snails according to Kerney et al. (1983) and Wiktor (2004).

Vegetation was described on the basis of phytosociological relevés using the Braun-Blanquet (1964) method. The relevés were taken at the spots where the mollusc samples were collected. The classification of plant communities follows Matuszkiewicz (2005). The phytoindication method was applied for the purpose of statistical analyses, using ecological index numbers proposed by Zarzycki et al. (2002) (L – light value, W – soil moisture value, T – trophy value, R – soil acidity (pH) value, H – organic matter content value). Plant indicator values had been successfully used previously as a tool for land mollusc autecology assessment (Horsák et al. 2007, Sulikowska-Drozd & Horsák 2007).

Average abundance, frequency coefficient and dominance were calculated for the mollusc assemblages. The following biodiversity indices were calculated: Shannon-Wiener diversity index (H), Pielou's evenness index (J), as well as average abundance and number of taxa for particular samples. For the above indices, statistical significance of differences between groups of samples with *V. angustior, V. moulinsiana* and other samples was tested with the Mann-Whitney test. Spearman's rank correlation coefficient was used to identify correlations between particular mollusc species and plant species. Cluster analyses were applied to analyse the zoocoenoses, based on the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) and Simpson's similarity measure. STATISTICA v. 10 INC StatSoft, PAST software was used for statistical tests and data analyses. The occurrence of molluscs was analysed in the context of vegetation and habitat parameters expressed as ecological numbers according to Zarzycki et al. (2002) and humidity scale according to Killeen & Moorkens (2003).

RESULTS

SPECIES RICHNESS AND COMPOSITION OF MALACOFAUNA

A total of 2,913 specimens representing 22 land snail species and three freshwater snail species were collected, as well as bivalves of the genus *Pisidium*.

The following representatives of the family Vertiginidae were identified: *V. angustior* (129 specimens; 5 sites), *V. moulinsiana* (4; 3), *V. antivertigo* (133; 15), *V. pygmaea* (204; 20), *V. substriata* (10; 2). Figure 1 shows the localities of the protected species (*V. angustior* and *V. moulinsiana*). Those localities were situated mainly along the Dziwna Strait and the Kamieński Lagoon, as well as on the Chrząszczewska Island; one site was located far from the banks of the Lagoon, near Lake Koprowo (site no. 22). No protected vertiginids were found in the environs of the Szczecin Lagoon. However, other vertiginid species were recorded there: *V. antivertigo*, *V. pygmaea* and *V. substriata*. In the collected material, the species with the highest dominance values were *Carychium minimum* (33%) and *Succinea putris* (17%). The frequency of *C. minimum*, *S. putris* and *V. pygmaea* exceeded 50%.

Taking into account only the seven localities with the protected vertiginids (Table 1), the list of species with over 10% relative abundance and over 60% frequency comprised *C. minimum* (37.3%, 100%), *S. putris* (12.6%, 100%) and *V. angustior* (11.6%, 71.4%). In the discussed group, other high-frequency species were *V. pygmaea* (85.7%), *V. antivertigo* (85.7%), *Galba trunca-*

Table 1. Mollusc species, their occurrence, dominance and frequency shown separately for sites with protected vertiginids and the remaining sites. Protected species bolded

Species	Abbreviation	Mean number of individuals/site		Dominance [%]		Frequency [%]	
		sites with protected vertiginids	other sites	sites with protected vertiginids	other sites	sites with protected vertiginids	other sites
Galba truncatula (O. F. Müller, 1774)	Gal tru	7.1	1.2	4.5	2.2	71.4	29.6
Anisus leucostoma (Millet, 1813)	Ani leu	0.1	1.4	0.1	2.6	14.3	7.4
Aplexa hypnorum (Linnaeus, 1758)	Apl hyp	0.0	0.7	0.0	1.3	0.0	11.1
Carychium minimum O. F. Müller, 1774	Car min	59.4	16.6	37.3	30.2	100.0	66.7
Carychium tridentatum (Risso, 1826)	Car tri	2.0	0.0	1.3	0.1	14.3	3.7
Carychium sp. juv.	Car sp	3.0	0.1	1.9	0.1	14.3	3.7
Succinea putris (Linnaeus, 1758)	Sus put	20.1	11.6	12.6	21.1	100.0	81.5
Oxyloma elegans (Risso, 1826)	Oxy ele	1.0	0.7	0.6	1.2	14.3	22.2
Succineidae juv.	Suc sp	1.4	1.3	0.9	2.3	28.6	22.2
Vallonia costata (O. F. Müller, 1774)	Val cos	0.0	0.5	0.0	0.9	0.0	7.4
Vallonia pulchella (O. F. Müller, 1774)	Val pul	3.1	1.4	2.0	2.6	71.4	29.6
Cochlicopa lubrica (O. F. Müller, 1774)	Coc lub	0.0	0.9	0.0	1.7	0.0	11.1
Cochlicopa nitens (M. von Gallenstein, 1848)	Coc nit	0.0	0.0	0.0	0.1	0.0	3.7
Cochlicopa sp. juv.	Coc sp	2.9	0.7	1.8	1.2	71.4	29.6
***Vertigo angustior* Jeffreys, 1830**	**Ver ang**	**18.4**	**0.0**	**11.6**	**0.0**	**71.4**	**0.0**
Vertigo antivertigo (Draparnaud, 1801)	Ver ant	10.6	1.5	6.6	2.8	85.7	33.3
***Vertigo moulinsiana* (Dupuy, 1849)**	**Ver mou**	**0.6**	**0.0**	**0.4**	**0.0**	**42.9**	**0.0**
Vertigo pygmaea (Draparnaud, 1801)	Ver pyg	5.1	5.4	3.2	9.8	85.7	51.9
Vertigo substriata (Jeffreys, 1833)	Ver sub	0.6	0.2	0.4	0.4	14.3	3.7
Vertigo sp. juv.	Ver sp	7.1	1.0	4.5	1.9	85.7	14.8
Vitrina pellucida (O. F. Müller, 1774)	Vit pel	0.0	0.9	0.0	1.7	0.0	25.9
Zonitoides nitidus (O. F. Müller, 1774)	Zon nit	6.7	1.5	4.2	2.7	57.1	40.7
Nesovitrea hammonis (Strøm, 1765)	Nes ham	1.3	1.0	0.8	1.9	28.6	29.6
Punctum pygmaeum (Draparnaud, 1801)	Pun pyg	5.1	3.1	3.2	5.7	71.4	44.4
Euconulus sp. juv.	Euc sp	1.1	1.1	0.7	2.0	57.1	44.4
Fruticicola fruticum (O. F. Müller, 1774)	Fru fru	0.1	1.2	0.1	2.2	14.3	14.8
Trochulus hispidus (Linnaeus, 1758)	Tro his	1.0	0.6	0.6	1.1	28.6	18.5
Arianta arbustorum (Linnaeus, 1758)	Ari arb	0.3	0.1	0.2	0.1	28.6	7.4
Cepaea hortensis (O. F. Müller, 1774)	Cep hor	0.4	0.1	0.3	0.1	14.3	7.4
Helicidae juv.	Hel juv	0.0	0.0	0.0	0.0	0.0	0.0
Pisidium sp.	Pis sp	0.6	0.0	0.4	0.0	14.3	0.0
	Total	159.4	54.8				

tula (71.4%), *Punctum pygmaeum* (71.4%) and *Vallonia pulchella* (71.4%). Compared to all the sampling sites, in those with protected vertiginids, *Cochlicopa lubrica, Vallonia costata, Vitrina pellucida, Oxyloma elegans*, and *Aplexa hypnorum* had lower frequencies.

In the localities with protected vertiginids, 12 mollusc species were recorded on average, and a sample collected by the standard method contained the mean number of 159 specimens (Table 2). Although the total number of taxa was higher in the remaining localities, the mean values of species richness and abundance per sample were two times smaller. The Mann-Whitney test revealed significant differences between the sites with protected vertiginids and the other sites, with respect to the number of species ($p = 0.0013$), abundance ($p = 0.0005$), and Shannon index ($p = 0.0043$). Only in the case of the evenness index no significant differences were found ($p = 0.0962$).

Table 2. Comparison of species richness and diversity: sites with protected vertiginids and the remaining sites

	Sites with protected vertiginids	Other sites
Number of sites	7	27
Total number of taxa	22	24
Average number of taxa	12	6
Average number of individuals	159	55
Shannon_H	1.850	1.036
Evenness_e^H/S	0.552	0.676

SNAIL CO-OCCURRENCE

The malacofauna found in the studied sites formed three quite clearly distinguishable groups (Fig. 2). In the first group *V. antivertigo* and *V. angustior* co-occurred with the hygrophilous *C. minimum*. The group included also two species which were, however, more loosely associated with it: *Zonitoides nitidus* and *Cochlicopa nitens*, both typical of very wet habitats and shores of water bodies. The second group comprised land snails typically associated with open habitats, such as meadows and nettle beds with a high moisture level but rarely inundated (*S. putris, Trichia hispida, Fruticicola fruticum, V. costata, V. pulchella, V. pellucida, Carychium tridentatum*). The only vertiginid species in that group was *V. pygmaea*. The third group comprised *V. moulinsiana* and *V. substriata* accompanied by freshwater molluscs of the genera *Galba, Anisus*, and *Pisidium*, and the euryoecious land snail *Nesovitrea hammonis*. The group also comprised a *Euconulus* (unidentified species; in the wetlands it was probably *E. praticola*).

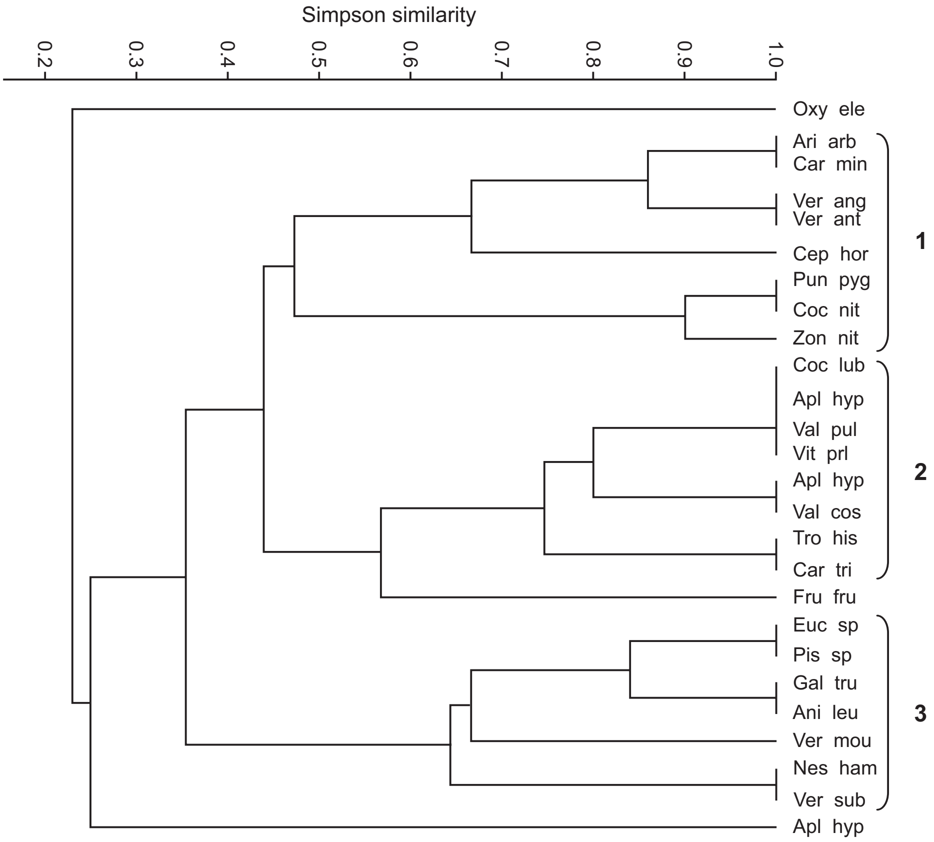

Fig. 2. Snail co-occurrence in cluster analyses based on the Unweighted Pair Group Method with Arithmetic Mean (UPGMA). For abbreviations see Table 1

PLANT OCCURRENCE AS AN INDICATOR OF VERTIGINID HABITATS

The plant communities in the sampling sites were *Phragmitetea* (*Phalaridetum arundinaceae, Caricetum distichae, Caricetum acutiformis, Caricetum gracilis, Phragmitetum australis*) and *Molinio-Arrhenethereta* (*Calthion* – community with *Deschampsia caespitosa; Arrhenatherion* – community with *Arrhenatherum elatius; Filipendulion – Lysimachio-Filipenduletum; Alopecurion – Alopecuretum pratensis*), a community with *Juncus effusus*, and a community with *Agrostis stolonifera*, as well as *Holcetum lanati*.

In the Odra River estuary, *V. angustior* and *V. moulinsiana* occurred in four plant communities: sedge beds *Caricetum gracilis*, *Caricetum distichae, Caricetum acutiformis* and herbs of the *Lysimachio-Filipenduletum* community (Table 3). None of the recorded plant species were present in all localities with *V. angustior* and *V. moulinsiana*, but *Filipendula ulmaria*, *Carex gracilis*, *Lathyrus palustris* and *Juncus effusus* were frequent.

HABITAT MOISTURE AND VERTIGINIDS

Species of *Vertigo* occurred in sites with moisture level ranging from 1 to 4 according to the applied scale. The protected *V. angustior* and *V. moulinsiana* were found only under "wet" and "very wet" conditions (5 and 2 sites, respectively). In the sites where the remaining vertiginids occurred, the moisture level was either lower (3 sites – "dry", 7 sites – "damp"), or comparable (7 sites – "wet"). The above values of field moisture indicator, showing the current ground water level in the studied sites, were positively correlated with the values of soil moisture indicators (W) calculated for those sites, based on the species composition and ecological preferences of plants providing insight into long-term habitat conditions ($r = 0.61$, $p < 0.05$). However, no statistically significant correlation was found between the soil moisture indicator (W) and the occurrence of any species of *Vertigo*. The same was true of other plant-based indicators.

Table 3. Vertiginids found in specific plant communities. Protected species bolded

Plant community	Sampling sites	*Vertigo* species (number of sites)
Caricetum gracilis	6, 7, 16, 20, 21, 28, 41, 52	***V. angustior*** (2),*V. pygmaea* (6), *V. antivertigo* (5)
Caricetum distichae	1, 4, 12, 17, 35, 49	***V. angustior*** (2),*V. pygmaea* (4), *V. antivertigo* (3)
Caricetum acutiformis	2, 5, 22, 34, 36, 40, 54	***V. moulinsiana*** (2),***V. angustior*** (1), *V. pygmaea* (4), *V. antivertigo* (3), *V. substriata* (1)
comm. with *Juncus effusus*	38, 51,53	*V. antivertigo* (1), *V. pygmaea* (1), *V. substriata* (1)
Alopecuretum pratensis	19, 25	*V. pygmaea* (1)
comm. with *Arrhenatherum elatius*	24, 27	*V. pygmaea* (2),*V. antivertigo* (1)
comm. with *Deschamspia caespitosa*	31	*V. pygmaea* (1),*V. antivertigo* (1)
Phragmitetum australis	23	*V. antivertigo* (1)
Lysimachio-Filipenduletum	14	***V. moulinsiana*** (1), *V. pygmaea* (1)
Holcetum lanati	26	*V. pygmaea* (1)

Table 4. Spearman's rank correlation between the respective mollusc and plant species. Shaded cells indicate a significant positive correlation ($p < 0.05$)

	Carex acutiformis	*Acorus calamus*	*Lotus corniculatus*	*Sonchus palustris*	*Chamaenerion angustifolium*	*Festuca rubra*	*Lychnis flos-cuculi*	*Polygonum bistorta*	*Equisetum fluviatile*	*Eriophorum angustifolium*	*Caltha palustris*	*Lathyrus palustris*	*Myosotis palustris*	*Cirsium arvense*	*Dactylorhiza majalis*	*Epilobium palustre*	*Plantago lanceolata*	*Poa palustris*	*Arrhenatherum elatius*	*Lotus uliginosus*	*Stellaria media*	*Lycopus europaeus*	*Peucedanum palustre*	*Poa pratensis*	*Ranunculus flammula*	*Rumex crispus*	*Alopecurus geniculatus*	*Trifolium medium*
V. moulinsiana	■	■	■	■	■	■																						
V. angustior		■	■	■	■	■	■	■																				
V. antivertigo						■	■	■	■	■	■	■	■															
V. pygmaea														■	■	■	■	■	■	■	■							
V. substriata																						■	■	■	■	■	■	■

DISCUSSION

In the Odra estuary, five out of eleven native species of the genus *Vertigo* were recorded, including two protected species: *V. angustior* and *V. moulinsiana*. The latter was collected only as singletons at three localities, which may result from mismatching the sampling method and the snail's microhabitat preferences. According to CAMERON et al. (2003) *V. moulinsiana* climbs tall plants during the vegetation season and can be found amongst litter only in winter, while MYZYK (2011) observed that in summer only the youngest juveniles stayed close to the ground surface. It is likely that the number of *V. moulinsiana* specimens detected in this study would be higher if an additional sampling method was used (i.e. shaking snails off the vegetation into trays; TATTERSFIELD & MCINNES 2003, LIPIŃSKA et al. 2012). In most sites with *V. angustior*, large sedge communities of *Magnocaricion*: *Caricetum distichae*, *C. gracilis*, *C. acutiformis* predominated; this was the case in sites 2, 4, 6, 16, 17, and 22 (Fig. 1). Such plant communities are characteristic of constantly moist and periodically flooded habitats (MATUSZKIEWICZ 2005). Records of *V. moulinsiana* were also made in communities with *C. acutiformis* and in one site (no. 14), where the dominant type of vegetation was meadow tall perennials: *Lysimachio-Filipenduletum*. That plant community developed in a well-drained habitat bordering on a belt of reed and sedge rushes. The small number of collected individuals does not allow to draw conclusions on the preferences of *V. moulinsiana* in the region. All of the above mentioned plant communities are either common or frequent in Western Pomerania (MATUSZKIEWICZ 2005). The only noteworthy community is *Caricetum distichae*, which usually occupies small areas and is present in the mosaic of plant communities in the studied area. *Carex disticha* is a low sedge growing in compact groups but forming no clumps, which is conducive to the development of species diversity in a habitat (TOMASZEWICZ 1979, own unpublished observations). Its communities are characterised by a higher access to light compared to others, providing favourable conditions for the development of a specific microbiome on sedge leaves, which may have an indirect positive effect on the occurrence of the vertiginids. A negative correlation of *V. angustior* with shaded microhabitats was also found in other studies (e.g. KSIĄŻKIEWICZ et al. 2013).

In the Odra estuary the protected vertiginids co-occurred with many plant species, confirming the literature data. According to KILLEEN (2003), *V. moulinsiana* was frequently found on tall monocotyledons such as *Glyceria*, *Carex* and *Phragmites*, but the list of plant species which the snails may climb is much longer (MYZYK 2004, KSIĄŻKIEWICZ 2010, LIPIŃSKA et al. 2011). In the studied area, floristic differences between the sites with and without vertiginids consisted mainly in the numbers of particular plant species: in drier sites such taxa as *Alopecurus* dominated and sedges were few, whereas in wetter places *Carex* dominated and *Alopecurus* occurred only sporadically.

The studies conducted so far on habitat preferences of vertiginids indicate that it is the structure of the vegetation rather than its species composition that plays an important part in the snail occurrence. *V. angustior* is most abundant in dense narrow grass habitats with deep thatch overlying well-drained soil within areas with high water table (KILLEEN & MOORKENS 2011). According to LIPIŃSKA et al. (2011) the occurrence of *V. moulinsiana* is associated with the spatial structure of vegetation under particular hydrological conditions, which allow for development of a specific microclimate. The studies conducted along the transect delineated by various habitats with vertiginids revealed that an almost complete spatial segregation, both horizontal and vertical, occurred between *V. moulinsiana* and *V. angustior* (JANKOWIAK & BERNARD 2013). The latter species preferred lower moisture level and was encountered mostly at microsites in thatch and litter, where it sometimes climbed parts of plants up to several centimetres high.

V. moulinsiana and *V. angustior* inhabit wetlands. *V. angustior* occurs in a damp intermediate zone between marshes and drier grasslands (KILLEEN & MOORKENS 2011). The range of habitat moisture preferred by *V. moulinsiana* is shifted towards very wet sites, where the water table is at, or slightly above, the ground surface (TATTERSFIELD & MCINNES 2003). According to the above authors, it is likely that the minimum summer water level is a critical characteristic of *V. moulinsiana* habitat. In the present study in the Odra estuary, *V. angustior* and *V. moulinsiana* were recorded in sites where the ground surface was damp during summer, although no water appeared when pressure was applied, while the vegetation indicated that water might periodically stagnate there.

The present-day character of habitats within the Odra estuary has been affected by drainage conducted since the 19th c. in connection with agricultural activities in the area. The extensive boggy plain beside the Szczecin Lagoon (basin of Basen Czarnociński: sites 29–44, bogs of Bagna Struskie: sites 53–55) has undergone extensive drainage which turned it into meadows and pastures. With time, the structure of vegetation in the area became simplified (reduction of mosaic character, appearance of species characteristic of degraded meadows) due to the presence of drainage ditches and the intensification of agricultural production during the period of functioning of State Agricultural Farms (JASNOWSKA 1995, NYC

1995). On the other hand, intensive exploitation of the narrow meadow strips beside the Kamieński Lagoon was not profitable, so they were drained to a lesser extent, and levees were built only sporadically. Since the areas were flooded for prolonged periods during the year, they had to be exploited more extensively, and heavy machines could not be used. In this way, comparatively narrow strips of meadows beside the river, which were not fit to be turned into polders and intensively exploited, could become refuges of the protected vertiginid species in the Odra estuary. The observations confirm those reported by other authors who found that vertiginids could inhabit a landscape greatly altered by human activities if the surrounding areas ensured constant dampness (Jankowiak & Bernard 2013). Especially *V. angustior* occurred in some occasionally or extensively used habitats and was not very sensitive to some kinds of human impact (Killeen 2003, Killeen & Moorkens 2011, Jankowiak & Bernard 2013). It was easier for *V. angustior* to survive an occasional summer mowing in a fen habitat, since the species lived mainly in thatch and litter (Jankowiak & Bernard 2013). *V. moulinsiana* seemed to be more sensitive to disturbances. It was shown that even extensive cattle grazing could lead to decreasing its densities in a tall-herb fen (Ausden et al. 2005). Snails are probably affected by direct trampling or grazing, but they also suffer from the shrinkage of areas covered with vegetation where they can feed and by opening up the vegetation which reduces the humidity amongst it.

The fact that the sampling sites were situated in the Odra estuary allows for making comparisons with the study on the occurrence of vertiginids in the River Blythe estuary in England (Killeen & Moorkens 2011). The authors recorded *V. angustior* along levees: at the foot of the levee, in the zone flooded during high tides, on the slope of the levee both on the water side and on the land side and also in the zones adjoining salt evaporation ponds and underbrush. The data indicated that *V. angustior* was not sensitive to increased salinity of ground water and soil. The species' preferred habitat was maritime grassland which required a contribution of salt spray. Likewise, in our study area, the protected vertiginid species were recorded in sites exposed to periodic flooding with brackish water, because high water levels in the Kamieński Lagoon and the Dziwna Strait accompanied the occurrence of sea-induced backwater current, which occurred there according to the same mechanism as in the Szczecin Lagoon (Kowalewska-Kalkowska 2012). The phenomenon was the most frequent at the boundary of autumn and winter, when very strong northern winds turned back the waters of the Dziwna River (Prawdzic & Flak 1982, Trzeciak et al. 1992). Normally, the water of the Dziwna Strait flowed north, but the backwater current made it flow south. The water level in the Kamieński Lagoon did not rise as significantly due to floods in the Odra River as due to the backwater current (Kowalewska-Kalkowska 2012).

Periodic flooding of habitats is conducive to dispersal of vertiginids. They can float on the surface membrane or travel on floating plant fragments. Myzyk (2011) observed that the large mantle cavity of adult *V. moulinsiana* and the air accumulated in it enabled the snails to float. Due to being waterborne, *V. angustior* and *V. moulinsiana* are able to successfully occupy relatively recently-created habitats (Killeen 2003, Killeen & Moorkens 2011). In Fig. 1 it can be seen that the sites with *V. angustior* and *V. moulinsiana* form a longitudinal line. Since the wet coastal areas are the most likely to be flooded as a result of the backwater current, the most probable location from which the vertiginids could migrate and colonise other sites was site 2, situated on the Karpinek Bay. The vertiginids were very abundant in that site (both species present), where high groundwater level was maintained throughout the year. All other sites where vertiginids occurred might be potentially flooded with the waters of the Dziwna Strait and the Kamieński Lagoon. Even the site situated farther inland on Lake Koprowo (no. 22) was connected with waters of the Lagoon through a lake and a canal. In spite of the presence of a functioning drainage system, it was well hydrated during the study period and characterised by a high floristic diversity. Colonisation of new habitats is probably facilitated by the fact that the Vertiginidae are capable of self-fertilisation (Pokryszko 1990b), so a single coloniser can establish a new population.

The distribution of vertiginids in the Kamieński Lagoon observed during the study probably resulted from dispersal during the periods when the backwater current caused water levels to rise. Passively dispersing snails established local populations wherever they encountered stable conditions with a high ground water level (they avoided drying out polders) and sedge vegetation.

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