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REPRODUCTION OF THE FRESHWATER SNAIL *VIVIPARUS CONTECTUS* (MILLET, 1813) (GASTROPODA: ARCHITAENIOGLOSSA: VIVIPARIDAE)

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ABSTRACT. Density, sex ratio, size structure and reproduction were analysed in populations of *Viviparus contectus* (Millet) from oxbows differently connected with the Bug River. The mean density was 20 ind./m^2, the sex ratio was 1:1. Snails of size classes II (8.1–12.0 mm shell width and height), III (12.1–25.0 mm width and 12.1–20.0 mm height) and IV (25.1–35.0 mm and 20.1–35.0 mm) were the most numerous. The youngest snails (shell height and width < 8 mm) were the least numerous. Smaller snails (class II) dominated in the spring. The proportion of classes III and IV increased in the summer and autumn. The number of embryos per female was the highest during the spring and summer – the period of intense reproduction. The number of embryos per female was the smallest (mean 6.8) in the oxbow isolated from the river; it was higher in the flow oxbows (13.6 and 14.2). In the isolated lake that number increased with the female's shell size. In the flow lakes the number of embryos was high irrespective of the female's size; females from these lakes showed the highest fecundity in all size classes. In the spring the mean number of embryos per female in classes II (11.5), III (12.4) and IV (14.6) was higher than in the largest females from the isolated lake. Similarly, in the summer the mean fecundity of females in class II (15.4 embryos/female) was higher than in the largest females in the lake isolated from the river (6.2).

KEY WORDS: *Viviparus contectus*, life history, population density, fecundity, size structure, sex ratio

INTRODUCTION

In Europe the freshwater family Viviparidae is represented by the genus *Viviparus* Montfort. *Viviparus contectus* (Millet, 1813) and *V. viviparus* (Linnaeus, 1758) are abundant in some benthic freshwater habitats in Poland. The former lives in vegetated shallow stagnant waters, on all types of bottom: stony, sandy, loamy or muddy. It can also occur in the current of small, slow-flowing rivers. Sometimes it co-occurs with *V. viviparus*. It is viviparous, iteroparous and dioecious, and shows a distinct sexual dimorphism.

The literature on various viviparid species in different habitats is fairly abundant (e.g. STAŃCZYKOWSKA et al. 1971, SAMOCHWALENKO & STAŃCZYKOWSKA 1972, YOUNG 1975, DE BERNARDI et al. 1976, BROWNE 1978, VAIL 1978, JOKINEN 1982, RIBI & GEBHARDT 1986, JAKUBIK 2003, 2006, 2007, JAKUBIK & LEWANDOWSKI 2007). Despite its being widespread in Europe (ZHADIN 1952), including Poland (PIECHOCKI 1979, FALNIOWSKI 1989), little is known of the life history of *V. contectus* (TAYLOR & ANDREWS 1991, ELEUTHERIADIS & LAZARIDOU-DIMITRIADOU 1995, RIBI & PORTER 1995, RIBI & KATOH 1998).

Long-term observations on *V. viviparus* revealed some life history traits which are stable and independent of the habitat type: the tendency to aggregate at the same time in the same places, the sex ratio and age structure, the proportion of fertile females in the populations. All of them guarantee maintaining a stable population density in the habitat. The number of embryos per female is, however, one of the variable traits and adjusts to habitat conditions (JAKUBIK in press). This paper, analysing life history traits in some populations of *V. contectus*, is an attempt to answer the following questions: 1. Does the predicted life strategy function unaltered in *V. contectus* from various aquatic habitats? 2. How would *V. contectus* change its adaptations to a definite set of environmental conditions?

MATERIAL AND METHODS

The studies were carried out in 2003–2007 in oxbow lakes of the Bug River: two flow lakes and one lake isolated from the river (Fig. 1). The Bug river is 772 km long; 184.4 km of its length being situated outside Poland. Its catchment area covers 39,200 km^2. The Bug is one of the few European rivers with preserved unaltered valleys and natural meandering channels along nearly the whole of their length. Its valley holds many oxbow lakes. Three of them were selected for this study (lakes near Wywłoka, Szumin and Lake Białe). The first two are ca. 20 ha in area, with the maximum depth of 4 m, and connected with the river on one end. In the 1980's Lake Wywłoka was divided in two parts by a dyke equipped with culverts. Lake Białe is ca. 1.5 ha in area, maximum depth 4 m, and is isolated from the Bug. Five sampling sites were selected in each lake.

Mollusc samples were collected in the near-shore zone in the spring, summer and autumn, with a dredge of 20 cm side, from 1 m^2 to the depth of 1 m, and in sites deeper than 1m with a dredge of 40 cm side. The material was washed on a 1 mm mesh sieve which enabled collection of viviparids of all size classes. The sex of each live individual was determined morphologically (PIECHOCKI 1979).

The snails were divided into juveniles, males and females. Juvenile shells were less than 8 mm high (size class I) and covered with characteristic hairs. Males and females were assigned to size classes based on their shell height and width measured with a calliper to the nearest 0.1 mm (class II 8.1–12.0 mm shell width and height, class III 12.1–20.0 mm width and 12.1–25.0 mm height, class IV – height > 25.0 mm, width > 20.0 mm). The females were dissected to determine their fecundity. They were divided into fertile (with embryos) and infertile (without embryos). The embryos were removed from the uteri and counted.

Apart from ANOVA, Chi square test was used to test the significance of differences between the studied parameters. Since the test revealed no differences between the sites and consecutive years in particular habitats, the results were presented as means. Spearman correlation was used to estimate the relationship between the mean number of embryos and shell height. The differences between the mean number of embryos, reproductive effort and season were tested with Newman-Keuls post-hoc test. Comparisons of sex ratio, percentage of fertile and infertile females and percentage of females in particular size classes between the habitats were done with the G test.

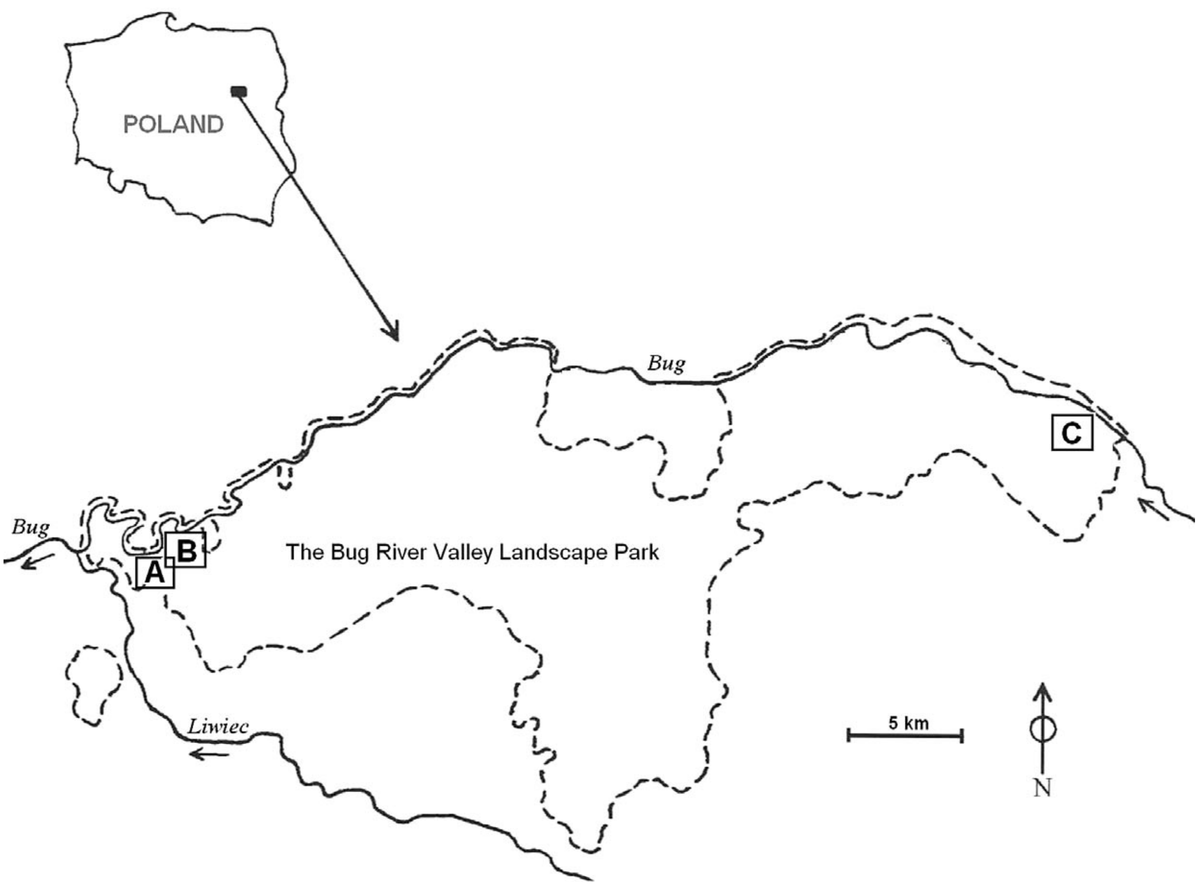

Fig. 1. Map of the studied lakes: Lake Szumin (A), Lake Wywłoka (B) and Lake Białe (C)

RESULTS

The snail density in particular sites of the studied lakes during the five years was similar and did not differ significantly. The mean density in the studied sites was 20 ind./m^2. The only differences in the density were those between seasons (Newman-Keuls test, p<0.001) (Table 1). The highest densities were observed in the spring and summer, in the autumn the density decreased. In the flow lakes the spring and summer densities did not differ significantly. In the isolated oxbow the densities varied with seasons (Table 2).

The sex ratio (females: males) in the studied sites was 1:1, with a slight predominance of males in the autumn (Table 3). The females were larger than the males (Fig. 2). The differences were statistically significant in lakes Białe (p<0.001) and Wywłoka (p<0.001). In Lake Szumin the males and females were of the same size (p=0.26). The largest females were found in Lake Białe (mean shell height 2.7 cm) and their height differed from that of females from Lake Szumin (p<0.001). No significant differences were found in shell heights between females from the other oxbows (p=0.07, p=0.13). The shell height of males was similar in the three oxbows (p=0.76, p=0.92, p=0.82).

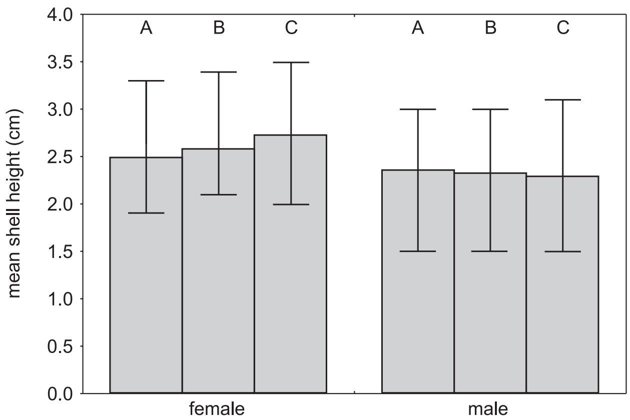

Fig. 2. Comparison of the mean shell height in female and male *V. contectus*. Vertical lines show range. For lettering see Fig. 1

Females of all size classes were present in the studied sites (Fig. 3). Snails of size classes II, III and IV were the most numerous; the youngest snails were the least so. Smaller snails (classes II and III) dominated in the spring. The greatest proportion of class II snails was noted in the flow lakes (up to 40%). In the sum-

Table 1. Density (ind./m^2) (mean±SD and range) of *V. contectus* in the studied lakes

Season/Lake	Szumin	Wywłoka	Białe
Spring	21.9±5.36	21.5± 5.70	20.8±5.59
	2–30	2–31	3–31
Summer	23.7±4.17	24.7±4.45	24.5±4.51
	9–35	11–34	10–37
Autumn	13.5±4.31	12.7±4.61	11.8±4.44
	6–22	3–22	4–21

Table 2. Statistical assessment of seasonal differences in snail density in the studied lakes

Lake/Season	spring–summer	spring–autumn	summer–autumn
Szumin	ns	df = 114, p<0.001	df = 125, p<0.001
Wywłoka	ns	df = 115, p<0.001	df = 134, p<0.001
Białe	df = 125, p<0.001	df = 123, p<0.001	df = 112, p<0.001

Table 3. Number and percentage of females and males in the spring (1), summer (2) and autumn (3) in the studied lakes

Sex	Season	Lake			*G*-test (df=3)
		Szumin	Wywłoka	Białe	
♀	spring	187 (52%)	198 (51%)	200 (49%)	1/2 4.30
	summer	190 (51%)	187 (50%)	192 (48%)	2/3 8.12
	autumn	193 (48%)	197 (49%)	200 (48%)	3/1 2.20
♂	spring	175 (48%)	190 (49%)	205 (51%)	1/2 7.50
	summer	185 (49%)	185 (50%)	198 (52%)	2/3 5.60
	autumn	210 (52%)	200 (51%)	214 (52%)	3/1 3.40

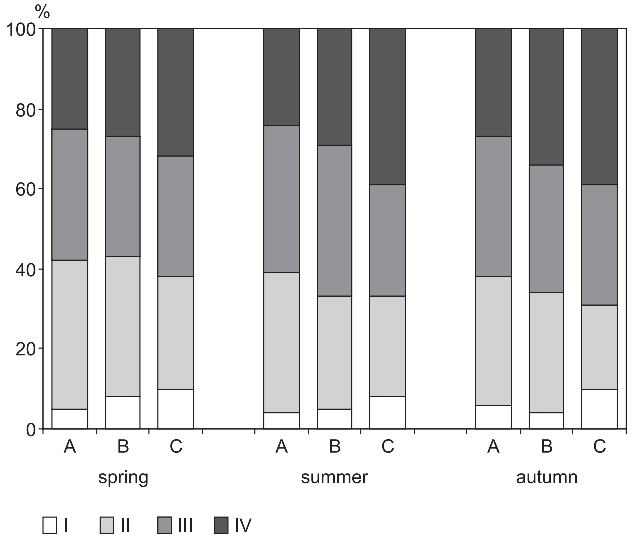

Fig. 3. Seasonal changes in size structure of female *V. contectus* in the studied lakes. For age classes (I–IV) see text

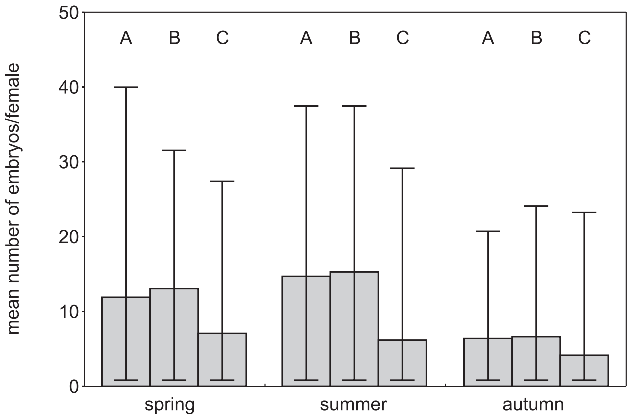

Fig. 4. Seasonal changes in the mean number of embryos per female of *V. contectus* in the studied lakes. Vertical lines show range. For lettering see Fig. 1.

mer and autumn the percentage of IV class snails increased which was particularly distinct in the isolated oxbow (autumn up to 40%).

The mean number of embryos per female changed in the same way in all the sites (Fig. 4). It was the highest in the spring and summer – the period of intensive reproduction, and lower in the autumn (Newman-Keuls test, $p<0.01$). The mean number of embryos per female was the highest in the flow lakes both in the spring (14.6 and 15.8) and in the summer (17.7 and 18.4). In the flow lakes the number of embryos was high irrespective of the female's size (spring $r_S=0.10$, summer $r_S=0.09$, autumn $r_S=-0.20$, $p<0.05$). In Lake Białe, however, the mean number of the last stage embryos (embryos with developed shell) increased with the female's shell height ($r_S=0.65$).

Embryos were present in females of size classes II, III and IV. In most sites the fecundity differed significantly among the size classes (Table 4). In all size classes females from the flow lakes were the most fertile. In the spring the mean number of embryos per female in classes II (11.5), III (12.4) and IV (14.6) for females from the flow lakes was higher than or similar to that in the largest females from the isolated lake (Newman-Keuls test, $p<0.001$). A similar situation was also observed in the summer when class II females from the flow lakes had more embryos (mean 15.4) than the largest females from the isolated lake (mean 6.2) (Newman-Keuls test, $p<0.05$).

Table 4. Comparison of the mean number of embryos/female in three size classes (II, III, IV) in the studied lakes. Significance: *$p<0.05$.

Lake	Size class	Spring		Summer		Autumn	
		Mean±SD	Newman-Keuls test	Mean±SD	Newman-Keuls test	Mean±SD	Newman-Keuls test
Szumin	II	11.5±2.91	II/III, II/IV*, III/IV*	12.0±2.50	II/III, II/IV*, III/IV	5.1±1.54	II/III,
	III	12.4±8.19		13.1±5.35		6.1±2.21	II/IV*,
	IV	14.6±4.11		14.0±9.14		8.1±3.11	III/IV*
Wywłoka	II	12.0±3.71	II/III*, II/IV*, III/IV*	15.4±3.13	II/III*, II/IV*, III/IV*	5.3±2.85	II/III, *
	III	15.1±9.15		18.2±5.19		7.9±3.41	II/IV*,
	IV	16.1±9.41		19.3±10.70		11.3±4.51	III/IV*
Białe	II	4.5±6.23	II/III*, II/IV*, III/IV*	6.2±3.23	II/III*, II/IV*, III/IV*	3.3±1.17	II/III,
	III	9.3±3.21		10.8±5.77		4.7±2.76	II/IV, *
	IV	12.6±9.63		13.5±9.02		8.1±1.22	III/IV*

DISCUSSION

Aggregating in the littoral zone is a typical habit of freshwater snails such as *Bithynia tentaculata* (L.), *Potamopyrgus antipodarum* (Gray), *Valvata piscinalis* (Müll.), *Viviparus viviparus* (L.) and *V. contectus* (Mill.) (PIECHOCKI 1979, KRODKIEWSKA et al. 1998). Aggregations of *V. viviparus* are formed in the summer; in the autumn the snails disperse along the shoreline and move deeper into the lake to overwinter buried in the mud. In the spring, the surviving individuals move towards the shore to form aggregations in the same places in the summer. The highest densities observed in the summer in such clusters exceed 1,000 ind./m^2 (e.g. ZHADIN 1928, 1952, FRÖMMING 1956, MIROSHNICHENKO 1958, STAŃCZYKOWSKA 1959, 1960a, b, SAMOCHWALENKO & STAŃCZYKOWSKA 1972, LEVINA 1992, ZHOCHOV 1993, ZETTLER 1996, JAKUBIK 2003). High densities are also typical for other viviparid species, e.g. several hundred ind./m^2 for *Viviparus malleatus* (Reave) in lakes near Montreal (STAŃCZYKOWSKA et al. 1971, 1972), *V. georgianus* (Lea) in North America (CLENCH 1962) and in lakes near New York (BROWNE 1978), *Cipangopaludina chinensis* (Gray) in Lake Connecticut (JOKINEN 1982) or even 1,500 ind./m^2 for *Viviparus ater* (Cristofori et Jan) in Lake Alserio in northern Italy (DE BERNARDI et al. 1976).

In the three oxbow lakes of the Bug River *V. contectus* did not form such dense aggregations; the mean density was 12 ind./m^2 in the autumn and 25 ind./m^2 in the summer, and was ten times lower than the density of *V. viviparus* in the flow lakes but comparable to that in the isolated lake (JAKUBIK et al. 2006). The difference is a result of habitat preferences of the two species. *V. viviparus* prefers rivers and flooded areas while *V. contectus* is more often found in stagnant water bodies, though the two species can co-occur. This pattern of occurrence has been suggested by ZHADIN (1928), based on his studies on viviparids in the Oka River basin. It is not always true in Poland (FALNIOWSKI 1989). In the oxbow lakes of the Bug River both species co-occurred, but in different densities. *V. viviparus* dominated in the flow lakes and *V. contectus* – in the isolated lakes. The studied lakes are astatic water bodies. Despite their similar origin, area, relatively small depth and initial water quality, after many years of functioning the lakes show a clear limnological identity. They are irregularly variable. All are situated in an agricultural landscape. Their water and bottom sediments are affected by the hydrological regime. Lakes Szumin and Wywłoka are connected with the Bug and, in the spring, are flooded with river waters which bring many *V. viviparus*, thus contributing to the local viviparid population. No river viviparids are introduced in Lake Białe, which was separated from the river long ago by the flood banks. Only single individuals of *V. viviparus* were noted there while *V. contectus* was numerous. Comparable densities of *V. contectus* have been recorded by ELEUTHERIADIS & LAZARIDOU-DIMITRIADOU (1995) for a Greek population from the wetlands of the Strymonas River.

The sex ratio in the studied populations of *V. contectus* differed from that in other viviparids (*V. malleatus*, *V. ater*, *V. viviparus*), whose populations were dominated by females (up to 80%) in the spring and summer during intensive reproduction. The number of males in those populations increased in the autumn when the sex ratio became established at 1:1 (e.g. STAŃCZYKOWSKA et al. 1971, DE BERNARDI et al. 1976, RIBI & PORTER 1995, JAKUBIK 2007). In the three oxbows of the Bug River the sex ratio was 1:1 with a slight predominance of males in the isolated lake. A similar sex structure has been reported by ELEUTHERIADIS & LAZARIDOU-DIMITRIADOU (1995) in a Greek population of *V. contectus*. According to FALNIOWSKI (1989) populations of this species are usually dominated by females but the sex ratios of 1:1 or male predominance have also been noted.

The distribution of size classes was similar in all the sites. The proportion of youngest snails was the highest in the spring. In the summer and autumn the proportion of medium-sized and largest snails increased as a result of growth. *V. contectus* has a differentiated embryonic growth but if young snails are not born in the autumn, they will be released from the breeding pouch in the spring next year (FALNIOWSKI 1989, ELEUTHERIADIS & LAZARIDOU-DIMITRIADOU 1995). Subsequent growth observed in the flow oxbows was so rapid that the snails attained class II size during the first two months of life (JAKUBIK & LEWANDOWSKI 2007). *V. viviparus* bred in captivity attained class II size in half a year; its growth rate should be studied also in a lake habitat.

Female *V. contectus* are larger than males which is a consequence of the species' viviparity. The literature provides many examples of the increase of the number of embryos and their development advancement with the female's size (SPIGHT 1976, FALNIOWSKI et al. 1996, MIDDELFART 1994, 1996, CHUNG et al. 2002): the largest females carry the highest number of fully developed embryos while in the smallest females single, least developed embryos are sporadically noted. I found a similar relationship in the isolated Lake Białe where the mean number of embryos in the last growth stage (embryos with developed shell) increased with the female's shell height and body mass. Such a regularity has also been noted by TAKI (1981) for *Cipangopaludina japonica* and by ESTEBENET (1998) for *Pomacea canaliculata* (Gastropoda: Ampulllariidae). A high shell provides adequate space for the snail's body with the oviduct filled with shell-covered embryos.

The fecundity differed among the three studied lakes. The mean number of embryos per female was 13 in the flow lakes and 6.4 in the isolated lake. The fecundity was average for the species. Literature data report 15–30 embryos per female (SAMOCHWALENKO & STAŃCZYKOWSKA 1972). The values are similar to those for other viviparids. FRÖMMING (1956) has noted 10 embryos per female in *V. viviparus*, RIBI & GEBHARDT (1986) – 15–20 in *V. ater* from Lake Zürich and Lago Maggiore, and TAKI (1981) – 10–20 in *Cipangopaludina japonica*. Much higher maximum numbers of embryos per female are given by JOKINEN (1982) for *Cipangopaludina chinensis* (102–162 embryos); PIECHOCKI (1979) reports on one case with over 80 embryos in *V. viviparus*, with the mean of 20, and FALNIOWSKI (1989) for the same species – on 24 to 73 embryos per female, with the mean of 50.

In the flow lakes the fecundity of *V. contectus* from size class II was higher than that of larger females from the isolated oxbow. According to FRÖMMING (1956) Viviparidae in Central Europe attain sexual maturity in the second year of life, but 90% of them do not contain embryos. The unstable habitat of the flow lakes may cause earlier reproduction of *V. contectus*. A similar situation has been observed for a natural population of *V. viviparus* in the same habitats (JAKUBIK in press) and for snails kept in the laboratory (JAKUBIK & LEWANDOWSKI 2007). Different conditions in the two types of habitats – flow and isolated lakes – mainly affect fecudinty and maturation of *V. contectus*. This is associated with food availability which is decisive for snail condition.

The content of organic matter, phosphorus and nitrogen in the bottom sediments varies among the studied lakes. They are abundant in the bottom sediments of the isolated Lake Białe; compared to the other two lakes the content of phosphorus in that lake is 2–3 times higher, and of nitrogen and organic matter – several times higher (JAKUBIK et al. 2006). Such good nutritional conditions might suggest a larger fecundity of the snails. Like *V. viviparus*, *V. contectus* takes most of its food with the radula and filtration is only a facultative way of feeding (FRETTER & GRAHAM 1978). However, in Lake Białe, with its abundant organic matter of terrestrial origin, the conditions for filtration are less favourable. The sedimentation rate is the highest in the autumn, while the reproduction of *V. viviparus* is at its peak in the spring and summer. The fecundity of the snails from Lake Białe is markedly lower than the average for Viviparidae.

The connection with the Bug River results in the habitat conditions in the two oxbow lakes being less stable. Since the snails feed mainly on organic matter, intensive feeding should follow an increase in its content in that period. The sedimentation rate of organic matter in the lakes connected with the river is higher in spring than in autumn (PORĘBSKI 2006) due to the matter inflow with flood waters. Organic matter content is, however, smaller in these lakes compared to isolated ox-bow lakes. This may be the reason of intensive feeding at the beginning of the vegetation season, when the snails use the increased resources of organic matter but later switch to algal food. This feeding pattern may also be associated with lower phytoplankton densities in spring due to its dilution by flood waters. The Bug River floods in March-April and its waters start to subside in early June.

Variable habitat conditions require an appropriate life strategy. ELEUTHERIADIS & LAZARIDOU -DIMITRIADOU (1995) have observed that, with decreasing temperature, *V. contectus* migrates to greater depths where they winter at a depth of 2 m. Similar migrations have been observed e.g. by SKOOG (1971) in *Theodoxus fluviatilis* (L.), HORST & COSTA (1975) in *Amnicola limosa,* and VINCENT et al. (1981) in *Bithynia tentaculata* (L.). A semelparous *Bithynia graeca* from an artificial Lake Kerkini (N. Greece) responds to rapid declines of depth and water volume with a high net reproduction and high growth coefficient (ELEUTHEIADIS & LAZARIDOU-DIMITRIADOU 2001). To persist in such a habitat *B. graeca* has to grow fast, have a short life cycle and a high production rate, and to allocate energy to reproduction. The earlier reproduction is probably an adaptation of *V. contectus* from the oxbow lakes to periodic floods. There are, however, some disadvantages to this reproduction pattern – the large energy expenditure for early reproduction may result in shorter life span (CZARNOŁĘSKI & KOZŁOWSKI 1998, CZARNOŁĘSKI et al. 2003, KOZŁOWSKI & TERIOKHIN 1999). Earlier maturation may be caused by the infection with digenetic trematode larvae. In some populations ca. 30% of female *V. contectus* are infected (SAMOCHWALENKO & StańczykOWSKA 1972), and females are more often infected than males (JEŻEWSKI 2004). The question needs further detailed investigation.

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