INVERTEBRATE REPRODUCTION IN ASTATIC WATER BODIES: EGG NUMBER – BODY WEIGHT RELATIONSHIP IN VIVIPARUS VIVIPARUS (L.) FROM OXBOW LAKES

ABSTRACT: Reproduction is the most important factor in population dynamics and invading freshwater habitats by Viviparus viviparus. This is largely associated with ovoviviparity of these snails. Some traits like steered reproduction, the appearance of young snails during the whole year, protection of embryos by female and delayed reproduction were fixed by natural selection as adaptations increasing the chance for progeny survival. In variable habitats like oxbow lakes seasonally joined to the river channel, Viviparidae start reproducing in the early stage of their life hence increasing a chance for population to survive.

Studies on fecundity, embryonic development of V. viviparus and the relationships between these parameters and females’ body size and weight, were carried out in oxbow lakes periodically connected to the river (the Bug River, Central Poland). The Bug River is one of a few European rivers which preserved their nearly natural character. No larger hydrotechnical works have been made in its valley, therefore, the river flows in a natural, meandering channel and forms numerous oxbow lakes. The surrounding of studied oxbow lakes is flat and of lowland character with mixed land use structure (arable lands, grasslands, settlements). Oxbow lakes are fed by the runoff from flood terrace, hence their waters are more fertile than those of the river. Two lakes were selected: Lake Szumin, area 17 ha, Lake Wywłoka – area 23 ha. Maximum depth of both lakes is ca 3 m. Samples of V. viviparus were collected in the years 2003–2007 with a bottom drag during the successive seasons from five sites in each oxbow lake. The embryos were found in females of the II (8.1–12.0 mm of width and height), III (12.1–20.0 mm width and 12.1–25.0 mm height) and IV (over 25.0 mm height and over 20.0 mm width) size classes. Three developmental stages were distinguished in embryonic growth: the oval transparent egg capsules (called the youngest embryos), egg capsules with visible contour of a shell (called medium embryos) and snails with a shell (the oldest embryos). The youngest growth stages of embryos (in a form of oval transparent egg capsules) dominated in all size classes of females. Medium growth stages (egg capsules with visible outlines of the shell) and the oldest ones (with shell) were represented in smaller proportion. The highest number of the youngest embryos per female were found in females of the II size class. The proportions of the embryo growth stages varied seasonally. The number of embryos per female and the degree of their development increased with the increase of shell (height, width, dry weight) and body (dry weight) parameters. High fecundity of the youngest females of V. viviparus is probably an adaptation to unstable habitat conditions of oxbow lakes.

KEY WORDS: Viviparus viviparus, embryonic development, size structure, fecundity, oxbow lake
1. INTRODUCTION

Naturally meandering river is able to change the course of its channel and to form numerous bends and closed meanders. While shortening its course a river forms oxbow lakes which are important elements of the river valley (Ward et al. 2002). The Bug is the largest river in eastern Poland. It is a borderline between Poland, Ukraine, and Belarus and finally discharges into the Zegrze Reservoir (Kondracki 1998, Kajak 1990, Dojlido et al. 2003). The Bug River is one of a few European rivers that did not undergo larger hydrotechnical works and, therefore, it flows in a natural, meandering channel forming numerous terraces, peninsulas, and islands typical of large lowland river of mineral substratum. The Bug River Valley is one of the best preserved valley landscapes of high natural values in Europe (Dombrowski et al. 2002). Oxbow lakes of the Bug River are situated on the first flood terrace built of gravel, sands, alluvial deposits and peat. Due to habitat heterogeneity the oxbow lakes are interesting study objects. Compared with the main river channel, the oxbow lakes are different aquatic habitats which is reflected in e.g. the sedimentation rate (Dawidek and Frencz 2005). The main factor affecting sedimentation is the river’s hydrological regime (Tockner et al. 1999, Ward et al. 2002, Obolewski et al. 2009). Lakes connected with the river are flooded in spring which results in higher sedimentation rate in this season. Oxbow lakes isolated from the river show larger sedimentation in autumn. This pattern produces different food conditions for organisms living in oxbow lakes. Unstable habitat conditions of oxbow lakes enforced many adaptations in these organisms.

Organisms developed many physiological, morphological and behavioural adaptations to variable habitat conditions. All of them compose a life history of a species. The forms of sexual reproduction – oviparity, ovoviviparity and viviparity – are the examples of such adaptation. Oviparity is the form most often found in invertebrates and vertebrates; ovoviviparity and viviparity are relatively rare. It concerns also Gastropoda.

Many adaptations may be found in snails already at the early stage of development of fertilised eggs. Freshwater Caenogastropoda developed many ways of protecting laid eggs from environmental factors which is reflected in different number and morphology of eggs, their size, ways of their lying and attaching to the substratum (Falniowski 2001). These differences affect the survival of egg capsules and further growth of young snails. Larger eggs richer in reserve substances enable complete development of an individual inside the capsule. Further growth and survival depends on the size after hatching (Calow 1978).

Ovoviviparity is a frequent way of reproduction in Gastropoda. Fertilised eggs of these snails develop in the oviduct which is their only protection. Young snails hatch in an egg capsule or leave the parent’s body themselves. Most ovoviviparid species of Gastropoda live in sea waters. Freshwater ovoviviparid Gastropoda include Potamopyrgus jenkinsi, Valvata naticina and all species of Viviparidae. Calow (1978) is of the opinion that ovoviviparity of freshwater species is one of adaptations to specific freshwater habitats. Already mentioned variability of habitat conditions inhibited the development of small eggs poor in egg yolk. Consequently, eggs must have bigger yolk reserves and larger space for prolonged embryonic growth.

Snails of the freshwater superfamily Viviparidae produce single egg capsules which protect particular embryos stored in females’ uteri. Embryonic growth proceeds within the capsules (Fetter and Graham 1962) and ends up with the development of a snail with shell (Jokinen 1984, Falniowski 1989). Particular embryos are displaced in female’s oviduct. The oldest embryos – snails with developed shell – are situated in the outlet part of the oviduct. They are surrounded by egg capsule which breaks before or after birth (Alkriinskaja 1969). Ovoviviparity is a strategy that provides protection for young snails, hence its success depends on the survival of parents during the reproduction period. Parent’s size often decides upon the number of embryos and the degree of their development.

Several-year-long studies on the populations of V. viviparus in various types of aquatic habitats (dam reservoir, river, ecotones) showed the relationship between the number of embryos and their growth and the shell and body size of snails (Jakubik 2007).
Heavier and larger snails produced more embryos. Embryonic development was also associated with the size and weight of adult individuals. Therefore, an attempt was undertaken to assess fecundity and embryonic development in *V. viviparus* from unstable habitats like oxbow lakes and to compare it with other aquatic habitats. Performed studies and observations demonstrated an earlier maturation of viviparids in oxbow lakes (Jakubik 2011). Field and laboratory experiments (Jakubik and Lewandowski 2007) showed that *V. viviparus* attained maturity in the second year of life but was able to produce progeny not earlier than in the beginning of the third year which was also confirmed by e.g. Frömming (1956). Fecundity is often determined by environmental factors like food quality as shown by Stańczykowska and Magnin (1973) for *Cipangopaludina chinensis*, *Viviparus fasciatus* and *V. viviparus*, by the presence of parasites (Samochwałenko and Stańczykowska 1972) or by temperature changes associated with habitat seasonality (Jakubik 2003). In unstable habitats like oxbow lakes viviparids reproduced already in the second year of life. The second aim of this study was to answer which of these factors was the reason for earlier maturation and embryonic growth.

2. MATERIAL AND METHODS

The studies were carried out in the years 2003–2007 in two oxbow lakes periodically joined to the Bug River (Fig. 1). The lakes are situated in the Nadbużański Landscape Park in the Bug River valley. The Bug River is one of a few European rivers which preserved unchanged valley and natural, meandering channel. There are flood terraces, oxbow lakes, dunes and steep banks in the valley (Walczak et al. 2001).

Two oxbow lakes were selected:

- Lake Szumin – an area of 17.0 ha and maximum depth of ca 4 m. The lake is connected with the river and a natural escarp was used to build flood embankment in the 1980s. Recently, the river has found a new connection to this lake. The lake is surrounded by grasslands and its southern shore is built up with holiday estates.
- Lake Wywłoka – an area of 23.4 ha and a maximum depth of ca 3 m. In the 1980s it was cut with a dike equipped with culverts. Western arm of the water body is open to the Bug River. Its catchment is dominated by meadows and pastures with small thickets. There is a holiday estate on southern lake shore. The lake is joined to the Bug River.

Fig. 1. Map of the study area: through-flow oxbow lakes (A – Lake Szumin, B – Lake Wywłoka).
Samples of molluscs were collected with bottom drags of various sizes in the shore zone in spring (April, May), summer (June-August) and autumn (September-October). Collected material was washed on a sieve with 1 mm mesh size which allowed obtaining retained all size classes of viviparids. Two species - *V. viviparus* and *V. contectus* were found in the study oxbow lakes. Differences between the two species were estimated according to Falniowski (1989).

The sex of every live individual was determined based on differences in the morphology between males and females (Piechocki 1979). Snails were divided into young, males and females. Young snails were less than 8.0 mm long (I size class). Females were separated according to size classes based on shell height and width measured with callipers to the nearest 0.1 mm (II class 8.1–12.0 mm of width and height, III class – 12.1–20.0 mm width and 12.1–25.0 mm height, IV class – over 25.0 mm height and over 20.0 mm width). This division was complemented with the determination of winter rings (Jakubik and Lewandowski 2007). The first ring appears when the shell height is of the II and III size class i.e. in the second year of life. The second ring corresponds to the III size class and the remaining rings (third to sixth) – to the fourth size class. It thus appears that the first size class includes snails in the age of one to several months which in the middle of the year grow up to the second size class. In the second year, snails have one winter ring and grow up to the III size class in the middle of this year. Sex is recognizable in the second year of life. The second winter ring appears in the third year and snails attain the IV size class.

Females of *V. viviparus* were dissected to determine their fecundity. The bodies of all females were removed from shells to isolate their oviduct under microscope. Then, embryos were taken out from oviducts and the number of embryos in particular growth stages was counted. Growth stages were distinguished upon their arrangement in the oviduct and the degree of development. In the initial part of the oviducts there were oval, transparent egg capsules (hereafter called the youngest embryos), in the middle part – egg capsules with visible shell outlines (hereafter called the middle–age embryos) and in the outlet part there were capsules containing fully developed snails with shell (called the oldest embryos). Linear size of shells of the oldest embryos (height and width) was determined under microscope equipped with micrometric scale in the ocular.

After blotting on a filter paper, females were dried at 60°C for 24 h to constant weight. Dried viviparids were weighed with an electronic balance CHYO YMC MK-50C to obtain dry body weight with shell (to the nearest 0.01 g) and dry weight of the shell alone with the same accuracy. The oldest embryos were also weighed with the accuracy of 0.001 g.

ANOVA and χ² test were used to estimate the significance of differences in analysed parameters between the two habitats (Łomnicki 1995). The test revealed a lack of statistically significant differences between lakes and study years (P = 0.75, P = 0.78). Differences between mean number of embryos per female in particular growth stages and between seasons were tested with Newman-Keuls test. Pearson's correlation was used to determine the relationships between the mean number of embryos (total and in particular growth stages) and shell height, shell width, dry body weight and dry weight of shells. Differences in dry weight, height and the number of whors of the oldest embryos between females size classes and seasons were checked with the Newman-Keuls test.

The *indirect index of reproductive effort* (IEI) was determined acc. to the equation given in Calow (1978):

\[
IEI = \frac{(E \times EV)}{SV}
\]

where: \(E\) – the number of embryos produced during the reproductive season; \(EV\) – embryo size (calculated as \(4/3 \pi r^3\) assuming the embryos are spherical); \(SV\) – parent's size (calculated as \(4/3 \pi r^3 h\) with the assumption that snails resemble the cone); \(r\) – embryo or shell radius, \(h\) – shell height.

3. RESULTS

The number of embryos per female did not show significant differences between study years and lakes (df = 5, \(\chi^2 = 8.47, P = 0.80\); df = 2, \(\chi^2 = 9.45, P = 0.80\)). This allowed for coupling the whole material and
Fig. 2. Changes in the mean number (for two lakes and all study periods *) of embryonic growth stages (a – oval, transparent egg capsules, b – egg capsules with visible outline of a shell, c – capsules with fully developed embryos with shell) in females of size classes II–IV in spring (A), summer (B) and autumn (C). *There is no significant differences between years and lakes ($P = 0.75, P = 0.78$) (see text).
making comparisons between females’ size classes. Embryos were found in females of the II, III and IV size class. The youngest embryos dominated (from 39% to 63%) in all females during the whole vegetation season. Middle-aged and oldest embryos were present in smaller proportions (from 19% to 34% and from 16% to 40%, respectively).

The highest mean number of the youngest embryos (25) was noted in summer in females of the II size class (Figs 2A, B, C). Mean number of the youngest embryos decreased with the increase in the size class of viviparids. Mean number of medium and oldest embryos was similar in the whole year. ANOVA showed the effect of season on the mean number of embryos in particular growth stages and in females’ size classes. Statistically significant differences were found in the mean number of the youngest embryos per female in all size classes of females between spring and summer (df = 215, P <0.001) and between summer and autumn (df = 209, P <0.001). Mean number of the oldest embryos per female of the II size class significantly differed between summer and autumn (df = 110, P <0.001) and between spring and autumn (df = 107, P <0.001). Statistically significant differences were also found for the mean number of the oldest embryos per female of the III size class between summer and autumn (df = 129, P <0.001) and between spring and autumn (df = 109, P = 0.025). Correlation coefficient showed the relationship between mean number of embryos and shell height and width, dry body weight and dry weight of the female’s shell. Mean number of embryos per female increased with the increase of these parameters. The strongest correlation was found between shell height and the mean number of embryos (r = 0.79, P <0.05).

The oldest embryos did not show significant differences in the dry weight, shell height and the number of its whorls between study years and lakes (df = 5, χ² = 7.67, P = 0.78;
df = 2, χ² = 8.35, P = 0.80), the differences were, however, found in females of various size classes (Table 1). These parameters of the oldest embryos were greatest in females of the IV size class. Shell height varied from 1.1 mm to 5.8 mm. The number of whorls varied from 1 to 3. Dry body weight varied from 0.004 g to 0.67 g. These parameters differed (with the exception of the dry body weight), however, between seasons. In spring they were largest in all size classes of females as compared with spring and autumn (Newman-Keuls test, P < 0.01). The number of embryos in particular growth stages was also correlated with these biometric indices. The mean number of the youngest, medium and oldest embryos increased with the increase of dry body weight of a female (r = 0.47, P < 0.05, r = 0.60, P < 0.05, and r = 0.99, P < 0.05, respectively). Dry body weight was the factor most significantly affecting the height of shells in oldest embryos (r = 0.95, P < 0.05) and the number of whorls (r = 0.99, P < 0.05). In various size classes of females this relationship was, however, different. In females of the II size class the mean number of embryos increased with shell height of females (r = 0.33, P < 0.05). Shell widths was correlated with the mean number of medium embryos (r = 0.48, P < 0.05) and with the number of shell whors of the oldest embryos (r = 0.40, P < 0.05). Dry females’ body weight was deciscive of the shell height (r = 0.51, P < 0.05) and width (r = 0.61, P < 0.05) of the oldest embryos. In females of the III size class the strongest correlations were noted between shell height of females and the mean number of embryos (r = 0.75, P < 0.05) and the mean number of the youngest embryos (r = 0.68, P < 0.05). Shell width of females in this size class of viviparids significantly affected the mean number of embryos (r = 0.51, P < 0.05) and the height (r = 0.55, P < 0.05) and width (r = 0.51, P < 0.05) of shells of the oldest embryos. In females of the IV size class the increase of shell height was associated with the increase of the height (r = 0.68, P < 0.050), width (r = 0.69, P < 0.05) and the number of shell whors (r = 0.73, P < 0.05) in the oldest embryos. The increase of shell width was followed by the increase of the mean number (r = 0.87, P < 0.05) and weight (r = 0.89, P < 0.05) of the oldest embryos. Dry body weight of females was also a determinant of the mean number of the oldest embryos (r = 0.96, P < 0.05), of the height (r = 0.97, P < 0.05) and width (r = 0.97, P < 0.05) of their shells and on their body mass (r = 0.95, P < 0.05).

4. DISCUSSION

Since body size of an individual increases the probability of its survival and affects its ability to produce progeny, it seems that the larger individual should produce more larger offsprings (Ziółko and Kozłowski 1983). This relationship was also found in snails (Roff 1992, Heller 2001). Individuals of larger body sizes accumulate bigger energetic reserves and may produce more progeny (Spight 1976, Middelfart 1994, 1996, Chung et al. 2002). This was confirmed in earlier studies on V. viviparus carried out in riverine habitats, in dam reservoir and in ecotone zones (Jakubik 2007).

Buckley (1986) remarked that the age of female of V. georgianus is a determinant of variable size of the young and of their future survival. Similar relationship was observed by Ribi and Gebhard (1986) in V. ater.

The analysis of embryonic growth stages in V. viviparus females of all size classes from studied oxbow lakes showed that most numerous in females’ oviducts were the youngest and medium-size embryos in spring, summer and autumn. They had particularly high percentage share in the smallest females in summer (over 60%). In a dam reservoir and in ecotone zones, a high percentage of the youngest embryos was found in the largest females in summer and autumn (Jakubik 2007). This may suggest the storage of embryos in females’ uteri for the next year. Embryonic development in Viviparidae is stretched over time. For example, a female of V. georgianus (Jokinen et al. 1982) is able to reproduce when attains the shell length of 15.5 mm i.e. at the age of 26 months. Embryos (usually 8) appear already in April as egg capsules. They are fed with proteins. An increase of temperature above 9°C causes further growth of embryos which lose protein shields in summer and by the end of September develop shells of a size of 2.6–4.1 mm. Young snails spend winter time in the oviduct of female. A high share of the youngest and middle-aged embryos dur-
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The whole year (and especially in spring) may be an evidence of constant reproduction and the production of a large number of progeny. Unstable habitat of through-flow oxbow lakes might cause such a reproduction pattern in *V. viviparus*. This strategy could be seen as a response to variable habitat conditions.

There were distinct differences between habitats where the fecundity of *V. viviparus* was analysed. These differences may result in different snail fecundity (Table 2). The Zegrze Reservoir is a complex and variable water body. As a through-flow water body it acts as a settling tank for seston delivered in its inflows (Jurkiewicz-Karnkowska, 2004). In the stagnant part of the reservoir concentrations of seston may vary in a short period of time due to enhanced sedimentation and a decline of water velocity (Kajak, 1990). Variable environmental conditions may decrease food availability or its assimilation which in turn may result in the observed smaller fecundity of viviparids.

Outlet river stretches are specific habitats rich in suspended matter and nutrients. Their high trophic status forms a habitat favourable for filter-feeders. Such conditions probably resulted in a high fecundity. In river, however, unidirectional flow makes nutrients and food particles less available for potential consumers. They are lost if not used at once (Reynolds et al., 1991).

Through-flow oxbow lakes are flooded in spring by waters of the Bug River which later retrieve part of the input matter back to the river channel. Small and relatively shallow oxbow lakes may functionally be compared to littoral which is the most diversified lake zone. Oxbow lakes accumulate organic matter produced *in situ* or delivered with surface runoff (terrestrial plant remains). Trophic status of these lakes is also affected by the inputs of organic and mineral substances from the river. All this may create favourable food conditions for freshwater Viviparidae.

Reproduction depends largely on habitat food resources. Since snails feed mainly on organic matter, intensive feeding should be a result of the increase of organic matter content. Sedimentation rate of organic matter in oxbow lakes joined to the river was higher in spring than in autumn (Porębski, 2006) due to flooding and the input of riverine matter in spring. This could be the reason of intensive feeding in the beginning of the vegetation season when snails utilised higher concen-

Table 2. Chemical characters of bottom sediments (concentrations of P – phosphorus, N – nitrogen; average annual 2003–2007) of studied water bodies: The Zegrze Reservoir (A), outlet river stretches (B), through-flow oxbow lakes (C) (Jakubik 2011, modified and present paper).

<table>
<thead>
<tr>
<th>Water body</th>
<th>Organic matter (% dry wt.)</th>
<th>P (mg g dry wt.)</th>
<th>N (mg g dry wt.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>0.97±0.60</td>
<td>0.20±0.11</td>
<td>0.77±0.52</td>
</tr>
<tr>
<td>B</td>
<td>29.74±0.17</td>
<td>0.60±0.26</td>
<td>7.58±0.80</td>
</tr>
<tr>
<td>C</td>
<td>5.10±2.62</td>
<td>0.14±0.14</td>
<td>4.39±5.03</td>
</tr>
</tbody>
</table>

Table 3. Changes in the indirect index of reproductive effort (IEI) (see formula 1) between spring (Sp), summer (Su) and autumn (Au) in the Zegrze Reservoir (A), outlet river stretches (B), through-flow oxbow lakes (C) (Jakubik 2011, modified). Significant differences (P <0.05) were bolded.

<table>
<thead>
<tr>
<th>Season</th>
<th>A Newman-Keuls test</th>
<th>B Newman-Keuls test</th>
<th>C Newman-Keuls test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring</td>
<td>0.26 (± 0.18)</td>
<td>0.40 (± 0.29)</td>
<td>1.63 (± 0.66)</td>
</tr>
<tr>
<td>Summer</td>
<td>0.38 (± 0.16)</td>
<td>1.45 (± 0.87)</td>
<td>5.05 (± 2.17)</td>
</tr>
<tr>
<td>Autumn</td>
<td>0.21 (± 0.12)</td>
<td>0.36 (± 0.15)</td>
<td>1.06 (± 0.24)</td>
</tr>
</tbody>
</table>
trematodes (from 7% in the Desna River. Jeżewski (2004) recorded 46% infection in snails from Ukraine and 28% infection in Lake Babje (2005) noted 28% infection in Lake Babje population infected by trematodes. Ivasuk by Nikitina (1986) who found 48% of snail from Lake Glubokoe (Russia) were obtained for Lake Mojtyńskie (Mazurian Lakeland) and in the Zegrze Reservoir to 31% infected in 30% infection by trematode larvae in Stańczykowska (1972) found over 50% infected by digenetic parasites. This regularity was confirmed in studies of Brown et al. (1988) and Synder and Esch (1993). Samochwalenko and Stańczykowska (1972) found over 50% infection by trematode larvae in V. fasciatus and 30% in V. viviparus in Lake Czerniakowskie, Lake Mikołajskie and in the Narew and Kru- tynia rivers. Similar results for V. viviparus from Lake Głubokoe (Russia) were obtained by Nikitina (1986) who found 48% of snail population infected by trematodes. Ivasuk (2005) noted 28% infection in Lake Babje (Ukraine) and 46% infection in snails from the Desna River. Jeżewski (2004) recorded from 7% V. viviparus infected by trematodes in the Zegrze Reservoir to 31% infected in Lake Mojtynskie (Mazurian Lakeland) and for V. contectus 10% population infected in Lake Mokre and 14% infected in Lake Czos.

Three species of trematodes were found in oxbow lakes: Amblosoma exile, Neocan-thoparyphium echinatoides and Leucochloridiodermophra lutea. The number of trematode species was comparable to or slightly lower than those found in the literature. Samoch-walenko and Stańczykowska (1972) noted the infection of V. viviparus and V. fasciatus by representatives of two trematode families: Xiphiocercaridae, Echinocestomatidae and by Diastomum luteum. Jeżewski (2004) in the Zegrze Reservoir and in the Wieprz and Narew rivers recorded the infection of V. viviparus and V. contectus by six species of trematodes (A. exile, N. echinatoides, L. lutea, Paracoenogonioinus ovatus, Cercaria vesicu-losa, Cercaria pugnax). Ivasuk (2005) found three species of trematodes: Leucochloridiodermophra constantinae, Cercaria bolschwensis and the rediae from the subfamily Echinostomatidae in V. viviparus from dam reservoirs Kaniv and Babje on the Dnieper River. Kra-sutska (2006) in the same water bodies noted the infection of V. viviparus by two trematode species (L. constantinae, C. bolschwensis).

The greatest share in the infection of V. viviparus had N. echinatoides (ca 90%) and A. exile (ca 80%), L. lutea was the least abundant. No differences were found in the fecun-dity between not infected and infected females (Tukey test, P = 0.87). Mean number of em-bryos in a not infected female of V. viviparus was 16.7 and in an infected female - 14.4. The reason for that was probably a form of parasite (metacercariae) present in snails. Similar observations were made by Zbikowska (2006) in Lymnaea stagnalis infected by Echinoparyphium aconiatum. The trematode was present in a form of metacercariae which affect snails less than other forms. This would explain an insignificant effect of trematodes on the reproduction of V. viviparus in which only metacercariae were found. Studies by Samochwalenko and Stańczykowska (1972) on two viviparid species showed, however, that trematode infection decreased the fecundity of infected females from two to four times. The two cited authors found metacercariae, cercariae, furcocercariae, rediae and sporocysts in viviparid’s bodies. Such a divers-ity of invasive forms of parasites could de-crease the fecundity of their host.

Females’ shell size and body weight decided upon the number of embryos. Shell height had the greatest effect on the mean number of embryos. High shell provides appropriate space for snail’s body with oviduct filled with embryos at various growth stages. The number of the oldest embryos, the height and the number of whorls of their shells depended on females’ body weight. Reproducing females of larger biomass are able to invest more in both survival and growth of their embryos. Female produces nutritive substances for em-bryos (galaktogen, proteins, glycoproteins, free aminoacids and calcium) in protein gland (Fretter and Graham 1978, D’Asaro 1988, Miloslavich 1996, Rawlings 1994, 1999).
These substances are successively utilised by developing embryos (Alakrinskaja 1969). The larger is females' body weight - the more food is produced. The food assimilated by embryos in subsequent growth stages gives finally large embryos with shells. In that form the embryos are singly released by female to water. Studies on the population of V. viviparus from a dam reservoir showed that the mean number of the oldest embryos increased with shell height and width and with dry weight of female's shell. Dry weight of female's body was most closely associated with the youngest growth stage of embryos (oval, transparent egg capsules) (Jakubik 2007).

In snails from the dam reservoir there was a correlation between size and weight of females and the number of embryos in particular growth stages. The highest correlation coefficient was found for the largest females which confirmed the thesis of a positive relationship between female's biomass and investment in progeny. Viviparids from oxbow lakes, however, contained embryos being already in the II size class. The mean number of embryos per female was relatively high and similar to the fecundity of larger females (IV size class) from other sites e.g. from the Zegrze Reservoir (Jakubik 2011). Values of the indirect index of reproductive effort (IEI) indicate different effort of females of V. viviparus from various habitats (lowland dam reservoir, ecotones and oxbow lakes periodically connected with the river - Table 3). The IEI index for viviparids from oxbow lakes was markedly higher than those from other habitats. This is an evidence for a negative correlation between reproductive effort and individuals size. Reproductive abilities are a function of body size of adult animals in most freshwater snails (see e.g. Dillon 2000, Norton and Bronson 2006). This relationship was highly significant in all habitats except oxbow lakes. Such correlation was also noted in other representatives of Viviparidae. Buckley (1986) and Lee et al. (2002) reported that the age of female of V. georgianus determined variable size of its progeny and their future chance of survival.

Despite a high fecundity and the presence of all growth stages of embryos in females from oxbow lakes, embryonic development is not so strongly correlated with female's size and weight. This is a phenomenon of an early reproduction of not fully prepared individuals as a response to less stable habitat conditions of oxbow lakes.

According to Calow (1978) semelparous species risk the loss of many of their offspring and iteroparous species refrain from reproduction under unfavourable environmental conditions. The optimum strategy of iteroparous V. viviparus studied in oxbow lakes periodically connected with the river was an earlier reproduction.

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