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REPRODUCTION AS A VARIABLE LIFE HISTORY TRAIT IN FRESHWATER SNAIL *Viviparus viviparus* (L i n n a e u s, 1758) (Gastropoda: Architaenioglossa: Viviparidae)

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Abstract

Jakubik B.: Reproduction as a variable life history trait in freshwater snail *Viviparus viviparus* (L i n n a e u s, 1758) (Gastropoda: Architaenioglossa: Viviparidae). Ekológia (Bratislava), Vol. 30, No. 1, p. 79–90, 2011.

Studies on *Viviparus viviparus* populations were carried out in freshwater bodies: in a dam reservoir, in outlet river stretches and in oxbow lakes variously connected to the river. Sex structure, fertility (understood as the number of fertile females in the population) and reproduction were analysed. The sex ratio in *V. viviparus* changed during the vegetation period. The largest percentage of females was found in summer, with slightly less in spring and the least in autumn. Fertile female percentages were dominant in all habitats and were very high in spring and summer with up to 90% in through-flow oxbow lakes. The most numerous were viviparids of the II, III, and IV size classes. The youngest snails with shell height and width less than 8 mm were least numerous. Smaller snails of the II size class dominated in spring while the number of III and IV size class viviparids increased in summer and autumn. Most embryos were noted in females in spring and summer during their intense reproduction while the number of embryos was almost twice as low in autumn. The highest values of reproductive effort (the IEI index) were noted in all habitats in summer which differed markedly from those in spring and autumn. The lowest fertility of *V. viviparus* was found in an oxbow lake cut off from the river with a mean value of 4 to 12 embryos/female and in a dam reservoir which had a mean number of 4 to 13 embryos/female. Snails from through-flow oxbow lakes were more fertile at 8 to 25 embryos/female and also from outflow river sections at 7 to 25 embryos/female. The mean number of embryos increased with the female's shell size. The greatest fertility in through-flow oxbow lakes was found in females of the II and III size classes. In spring, the mean number of embryos per female of the II size class (16 embryos) and that of the III size class (17 embryos) from through-flow oxbow lakes was greater than or comparable with that found in the largest females in other habitats. However, in females of the IV size class the greatest number of embryos per female was found in viviparids from river outlets.

Key words: dam reservoir, oxbow lake, *Viviparus viviparus*, reproductive cycle, fecundity, size structure, embryos, iteroparity

Introduction

Natural selection which shapes life history traits of a species such as body size, maximum physiological longevity, growth rate, age at maturity, number and size of progeny, parental care and semelparity or iteroparity adapts them to environmental conditions. This adaptation forms various life styles. In iteroparous species the main element of reproduction strategy is the trade-off between current reproductive effort and future survival and reproduction (Reznick et al., 1990; Kozłowski, 1991, 1992). To accomplish these strategies, species already formed many adaptations during embryonic growth stages. Models presented so far indicate proportional increase in reproductive effort with age most likely decrease the chance of survival (Charnov, Schaffer, 1973; Schaffer, 1974; Pianka, 1970; Pianka, Parker, 1975; Caswell, 1982).

Since Cole's 1954 classic paper, there have been many papers in malacological literature presenting population models of freshwater molluscs (e.g. Calow, 1978; Eversole, 1978; Dillon, 2000). These models are most often the result of studies on the ecological and evolutionary importance of fertility or on the amount of energy allocated to reproduction (e.g. Browne, Russell-Hunter, 1978; Aldridge, 1982; Velecká, Jüttner, 2000; Czarnołęski et al., 2005).

Change of life strategy as an adaptation to a definitive set of environmental conditions are observable in the freshwater family Viviparidae. It currently occurs throughout the world except for South America where it can be found only as fossil remains (Falniowski, 1989a, b). In European snail fauna the family is represented exclusively by the genus *Viviparus* Montfort. One representative of this genus – *Viviparus viviparus* (L.) – is very common in freshwater habitats of Poland. It lives in large rivers, in lakes of the river floodplains and less frequently in lakes and heavily overgrown ponds on sandy, loamy silty or stony substratum. It can rarely be found in temporary water bodies and in small overgrown standing waters. This is a mid- and east-European species ranging from the Ural to Sweden and in France and the eastern part of Great Britain (Falniowski, 1989a). In Poland, it inhabits lowlands in the northern and central part of the country and also sporadically on the Baltic Sea shores. It can sometimes be found in southern Poland for example, in the man-made reservoirs of Silesia (Strzelec, 1993).

Viviparus is an iteroparous prosobranch snail characterised by dioecy and sexual dimorphism. Snails produce single egg capsules that protect particular embryos, with the females giving birth to single or several snails and before death – to all embryos (Frömming, 1956).

Viviparity is arguably of the greatest importance in the colonization of freshwater habitats by *V. viviparus*. Many traits associated with viviparity such as steered reproduction, the appearance of the young all year round, embryo protection by the female and delayed maturation resulted from natural selection as adaptations to increase the survival rate of progeny.

This paper probes "examines" the following questions:
- does the life strategy of this species operate in unchanged form in various types of aquatic habitats?
- and, how does this species change its adaptations when confronted by a definitive set of environmental conditions?

Fig. 1. Map of study area: Zegrzyński reservoir(A), outlet river stretches (B), through-flow oxbow lakes (C), oxbow lake isolated from the river (D).

Material and methods

Studies were carried out in four freshwater habitats: (1) in the Central Polish Zegrzyński dam Reservoir , (2) in outlet sections of the Bug, Narew and Rządza rivers (studies in the years 1995–2007) and (3) and (4) in oxbow lakes of the Bug river variously connected with the river – two through-flow water bodies and one cut off from the river channel (studies in the years 2003–2007) (Fig. 1). Detailed characteristics of the reservoir and of the three rivers flowing into it was presented in an earlier paper (Jakubik, 2003).

The Bug river is 772 km long. Its upper 184.4 km part flows outside Poland and its total catchment area is 39.2 thousand km^2. The Bug is one of the few European rivers which preserved an unchanged valley and naturally meandering channel along amost its entire watercourse. There are numerous oxbow lakes in the river valley. Three of these are lake Białe and two lakes near Wywłoka and Szumin villages which are the objects of this study. The two latter lakes cover about 20 ha each with a maximum depth of 4 m and they are connected to the river channel. In the 1980's, the oxbow lake near Wywłoka was divided by a dyke with culverts. Lake Białe with an area of 1.5 ha and maximum depth of 4 m is separated from the river. Five study sites were selected in each habitat.

Hydrochemical studies involved analysis of organic matter and the total phosphorus and nitrogen contents in the sediments (Table 1).

Molluscs were collected in the shore zone in spring, summer and autumn. To a depth of 1 m, they were sampled from 1 m^2 of the freshwater bed with a small drag 20 cm wide. At greater depths (beneath 120 cm) samples were collected with the larger drag width of 40 cm. Collected material was washed on a sieve with a mesh size of 1 mm thus capturing viviparids of all size classes. The sex of each individual was then determined macroscopically based on the intersexual differences of snail morphology (Piechocki, 1979).

Snails were divided into young, males and females. The shells of the young were less than 8 mm long (I size class) and were covered with characteristic hairs. Males and females were divided into size classes after calliper measuring of the height and width of their shells to the nearest 0.1 mm (II class – width and height from 8.1 to 12.0 mm; III class – width 12.1–20.0 mm, height 12.1–25.0 mm; IV class – shell height over 25.0 mm and shell width over 20.0 mm).

T a b l e 1. Characteristic of studied habitats: Zegrzyński reservoir (A), outlet river stretches (B), through-flow oxbow lakes (C), and isolated oxbow lake (D).

Habitat	Organic matter (% dry wt.$^{-1}$)	P (mg g dry wt.$^{-1}$)	N (mg g dry wt.$^{-1}$)
	in bottom sediments		
A	0.97 ± 0.60	0.20 ± 0.11	0.77 ± 0.52
B	29.74 ± 0.17	0.60 ± 0.26	7.58 ± 0.80
C	5.10 ± 2.62	0.14 ± 0.14	4.39 ± 5.03
D	24.37 ± 19.36	0.35 ± 0.18	60.30 ± 36.80

Females of *V. viviparus* were sectioned to determine their fertility. Fertile females with embryos and infertile ones without embryos were separated. Embryos were extracted from the "uterus" of fertile females and counted. Their dimensions were measured under the microscope with a micrometric scale in the ocular. This allowed measurement of the reproductive effort using the formula for indirect effort index (IEI) (Calow, 1978):

IEI = (E x EV) / SV where

E – the number of embryos produced during the reproductive season,

EV – embryonic size (calculated as $4/3\ \Pi\ r^3$ assuming the embryos are spherical SV – parent's size (calculated as $4/3\ \Pi\ r^2h$ with the assumption that snails resemble the cone); r = embryonic or shell radius, h = shell height.

Besides ANOVA, the chi square test was used to check the significance of differences between analyzed parameters. The results showed a lack of differences between sites and years in particular habitats and therefore mean values could be used in presenting results. Thus, outlet stretches of rivers can be dealt with as one habitat and the same approach was applied to the two through-flow oxbow lakes of the Bug.

The Spearman correlation was used to determine the relationship between the mean number of embryos and shell height. Differences between the mean number of embryos, the reproductive effort and season were checked with the post-hoc Newman-Keuls test. Among-habitat differences in sex structure, the percentages of fertile and infertile females and the percentages of females in particular size classes were established with the G test.

Results

Although females were more numerous than males. In all studied habitats, the sex ratio changed during the vegetative season. The highest percentage of females was found in summer (up to 82% in outlet river stretches), with slightly less in spring and the least in autumn (up to 50% in the reservoir and in outlet river stretches) (Table 2).

Fertile females of *V. viviparus* dominated in all habitats. Their number was high in summer and this differed significantly from that in spring and autumn (Table 3). There were no significant differences in the percentage share of fertile females between spring and autumn, except in the through-flow oxbow lakes. In these habitats, fertile females contributed 90% and 65% of the total female number in spring and autumn, respectively (Table 3). The differences were statistically significant.

Females of all size classes were present in the studied habitats (Fig. 2). Most of these were in the II, III and IV size classes while the youngest individuals (shell height and width < 8 mm) were least numerous. Smaller snails (II and III size class) dominated in spring. The

Fig. 2. Comparison of percentage share of fertile females in particular size classes (I–IV) in spring, summer and autumn in Zegrzyński reservoir (A), outlet river stretches (B), through-flow oxbow lakes (C), and in oxbow lake isolated from the river (D).

Table 2. Percentage share of females and males in spring (1), summer (2) and autumn (3) in Zegrzyński reservoir (A), outlet river stretches (B), through-flow oxbow lakes (C), and in isolated oxbow lake (D).

Sex	Season	Habitats				*G*-test (df = 3)
		A	B	C	D	
♀	1	516 (60%)	291 (60%)	213 (62%)	201 (63%)	1/2 7.30*
	2	670 (78%)	397 (82%)	269 (80%)	240 (75%)	2/3 10.12**
	3	430 (50%)	242 (50%)	207 (60%)	166 (52%)	3/1 3.80
♂	1	344 (40%)	194 (40%)	131 (38%)	118 (37%)	1/2 8.70*
	2	189 (22%)	87 (18%)	76 (22%)	80 (25%)	2/3 9.60**
	3	430 (50%)	242 (50%)	138 (40%)	153 (48%)	3/1 4.50

Significance: *$P < 0.005$, **$P < 0.001$.

Table 3. Percentage share of fertile and infertile females in spring (1), summer (2) and autumn (3) in Zegrzyński Reservoir (A), outlet river stretches (B), through-flow oxbow lakes (C), and isolated oxbow lake (D).

Sex	Season	Habitats				*G*-test (df = 3)
		A	B	C	D	
♀ fertile	1	309 (60%)	203 (70%)	191 (90%)	124 (62%)	1/2 6.30*
	2	522 (78%)	317 (80%)	202 (75%)	180 (75%)	2/3 9.20*
	3	236 (55%)	145 (60%)	**134 (65%)**	96 (58%)	3/1 4.80 **except for C 10.50****
♂ in-fertile	1	206 (40%)	87 (30%)	21 (10%)	76 (38%)	1/2 7.60*
	2	147 (22%)	79 (20%)	67 (25%)	60 (25%)	2/3 8.50*
	3	193 (45%)	97 (40%)	**72 (35%)**	69 (42%)	3/1 3.70 **except for C 9.80****

Significance: *$P < 0.005$, **$P < 0.001$.

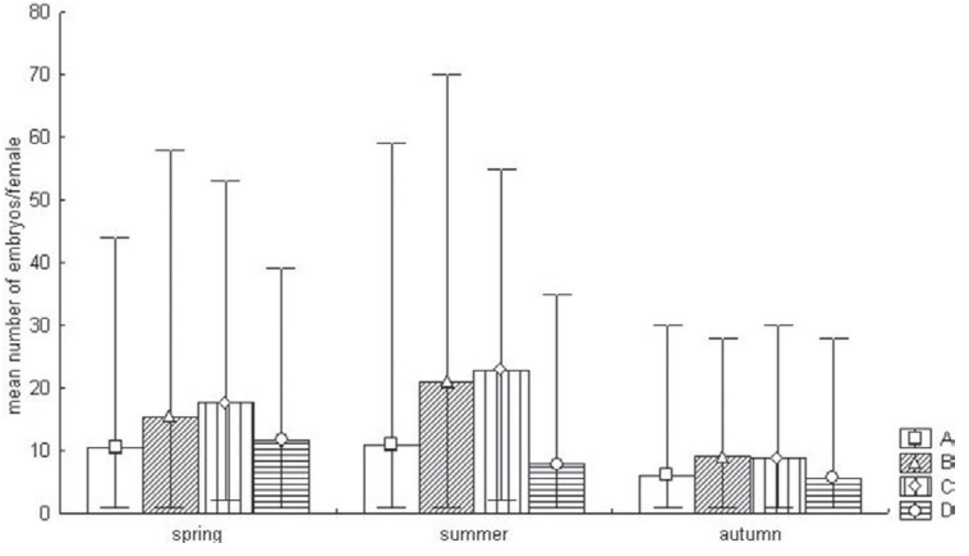

Fig. 3. Comparison of the mean number of embryos/female in spring, summer and autumn in Zegrzyński reservoir (A), outlet river stretches (B), through-flow oxbow lakes (C), and in oxbow lake isolated from the river (D).

greatest share of viviparids from the II size class (40%) was noted in through-flow oxbow lakes. In summer and autumn, viviparids of the IV size class became more numerous and this was particularly visible in an oxbow lake isolated from the Bug.

The mean numbers of embryos/female tended to change in a similar manner in all habitats (Fig. 3). The most embryos in females were noted in spring and summer during the period of most intensive reproduction, while the respective numbers in autumn were almost twice as small (Newman-Keuls test, $P < 0.01$). In spring and summer, the mean number of embryos/female was highest in through-flow oxbow lakes (15 and 23 embryos, respectively). However, the maximum mean numbers of embryos/female were found in outlet river stretches. Maximum values of the reproductive effort (measured as IEI) were noted in summer (in through-flow oxbow lakes) and these were significantly different from the respective values in spring and autumn in all studied habitats (Table 4).

The mean numbers of embryos/female were positively correlated with the females' size class. However, no such relationship existed in through-flow oxbow lakes where the number of embryos was high irrespective of the female's size (spring $r_S = 0.09$, summer $r_S = 0.06$, autumn $r_S = -0.06$, $P > 0.05$).

Embryos were present in females of the II, II and IV size classes although the fertility of *V. viviparus* females from most habitats differed significantly between size classes (Table 5). Only in autumn were no differences noted in through-flow oxbow lakes, while females of the II and III size class were most fertile from these sources. From females of the IV size class, most embryos were found in viviparids from outlet river stretches. In spring, the mean

T a b l e 4. Changes in the reproductive effort (IEI) between spring (Sp), summer (Su) and autumn (Au) in Zegrzyński reservoir (A), outlet river stretches (B), through-flow oxbow lakes (C) and in oxbow lake isolated from the river (D).

Season	A		Newman-Keuls test	B		Newman-Keuls test	C		Newman-Keuls test	D		Newman-Keuls test
	N	Mean (± SD)		N	Mean (± SD)		N	Mean (± SD)		N	Mean (± SD)	
Sp	250	0.26 (± 0.18)	Sp/Su*, Sp/Au, Su/Au*	190	0.4 (± 0.29)	Sp/Su*, Sp/Au, Su/Au*	105	1.63 (± 0.66)	Sp/Su*, Sp/Au Su/Au*	106	0.30 (± 0.15)	Sp/Su*, Sp/Au, Su/Au*
Su	324	0.38 (± 0.16)		201	1.45 (± 0.87)		136	5.05 (± 2.17)		130	0.44 (± 0.17)	
Au	286	0.21 (± 0.12)		101	0.36 (± 0.15)		104	1.06 (± 0.24)		98	0.26 (± 0.11)	

Significance: $^*P < 0.05$.

T a b l e 5. Comparison of the mean number of embryos/female in three size classes (II, III, IV) in Zegrzyński reservoir (A), outlet river stretches (B), through-flow oxbow lakes (C), and in isolated oxbow lakes (D).

Habitat	Size class	Spring		Summer		Autumn	
		Mean (± SD)	Newman-Keuls test	Mean (± SD)	Newman-Keuls test	Mean (± SD)	Newman-Keuls Test
A	II	4.5 (± 1.91)	II/III*, II/IV*, III/IV	7.0 (± 2.49)	II/III, II/IV*, III/IV*	3.7 (± 1.84)	II/III*, II/IV*, III/IV*
	III	12.4 (± 8.19)		10.1 (± 6.35)		7.1 (± 6.24)	
	IV	10.4 (± 8.18)		13.0 (± 11.14)		10.81 (± 5.61)	
B	II	8.0 (± 4.77)	II/III*, II/IV*, III/IV*	14.4 (± 7.63)	II/III, II/IV*, III/IV*	7.3 (± 3.85)	II/III, II/IV*, III/IV*
	III	19.9 (± 11.45)		17.6 (± 8.49)		7.8 (± 7.48)	
	IV	22.12 (± 11.45)		25.3 (± 15.70)		10.8 (± 5.61)	
C	II	16.5 (± 9.23)	II/III, II/IV*, III/IV	16.2 (± 8.73)	II/III*, II/IV, III/IV*	8.3 (± 4.17)	II/III, II/IV, III/IV
	III	17.0 (± 8.27)		25.8 (± 10.77)		9.6 (± 4.76)	
	IV	19.6 (± 11.63)		21.5 (± 12.02)		7.0 (± 5.22)	
D	II	4.4 (± 2.07)	II/III*, II/IV*, III/IV	7.15 (± 2.50)	II/III, II/IV, III/IV	3.56 (± 1.79)	II/III*, II/IV*, III/IV*
	III	12.0 (± 8.75)		7.0 (± 4.53)		6.4 (± 5.54)	
	IV	12.0 (± 8.75)		8.7 (± 4.63)		5.1 (± 4.27)	

Significance: $^*P < 0.05$.

number of embryos per female of the II size class (16 embryos) and the III (17 embryos) from through-flow oxbow lakes was higher or similar to that in females from other habitats (Newman-Keuls test, $P < 0.001$). This similar phenomenon was found in summer when the fertility of females of the II size class (mean 16 embryos) was higher than that of the largest females in the reservoir (mean 13 embryos) and also than those in the isolated oxbow lake (mean 9 embryos) (Newman-Keuls test, $P < 0.05$).

Discussion

Studies of *Viviparus viviparus* populations over several years have established some of their life history traits which are stable and independent of habitat type. These traits include the sex and age structure and percentage of fertile females in the population which guarantee an equilibrium in population density.

The sex structure in all studied habitats showed a similar pattern. Females dominated by up to 80% in spring and summer populations when snails reproduced intensively. In autumn the number of males increased to equalize the sex ratio. A similar change in the sex structure was reported by Stańczykowska et al. (1971) for *V. malleatus* from water bodies near Montreal, by De Bernardi et al. (1976), for *V. ater* from Lake Alserio in northern Italy and by Ribi (1999) for the populations of *V. ater* and *V. contectus* from lakes and rivers in northern Italy and Switzerland.

The highest numbers of embryos per female were found in summer, but these were slightly lower in spring and markedly less in autumn. Differences in the number of embryos per female between autumn and spring support the proposition that "winter" embryos begin life in early spring. More fertile females in spring than in autumn at the higher percentage share of females in the population provides evidence for their reduction in mortality during winter. This has also been noted in other Viviparidae e.g. in *V. georgianus* (Buckley, 1986), in *V. ater* (De Bernardi et al., 1976), and in *V. contectus* (Eleutheriadis, Lazaridou-Dimitriadou, 1995).

Reproduction differed in the four types of habitats studied. In summer, the mean number of embryos per female was 11 in the reservoir, 21 in outlet river stretches, 23 in through-flow oxbow lakes and 8 in the isolated oxbow lake. This data indicates that reproduction in all habitats maintained the average for this species (Samochwalenko, Stańczykowska, 1972). Frőmming (1956) reported 10 embryos per female for *V. vivparus*, while although Piechocki (1979) found as many as 80 embryos per female the mean number was only 20, and Falniowski (1989a) noted from 24 to 73 embryos per female, with a mean of 50. Meanwhile, 15–20 embryos per female were found in *V. ater* from Zürichsee and Lago Maggiore (Ribi, Gebhardt, 1986), and a much higher maximum of embryos per female were reported by Jokinen (1982) for *Cipangopaludina chinensis* at 102–162 embryos.

Obtained values of the IEI index here suggest a different reproductive effort in *V. viviparus* from the reservoir and from outlet river stretches, while the index for viviparids from through-flow oxbow lakes was markedly higher than that for snails from other habitats.

The concentrations of organic matter, phosphorus and nitrogen differed between the freshwater bed sediments in the studied aquatic habitats (Table 1). They were most abundant in river outlets and in lake Białe – an isolated oxbow lake – indicating ideal food conditions which could result in greater snail fertility. *V. viviparus* obtains most of its food with a radula and filtration remains its facultative feeding mechanism (Freter, Graham, 1978). Habitat is the main determinant of feeding methodology in *V. viviparus* (Jakubik, 2009). Outlet river stretches rich in nutrients and suspension carried in river waters are favourable sites for filter feeders such as *V. viviparus*. This is confirmed by the high fertility in this species. However, in lake Białe which is an oxbow lake isolated from the river, organic matter in sediments originates from the catchment basin and this provides less favourable conditions for filter feeders. The sedimentation rate in lake Białe is highest in autumn and *V. viviparus* reproduces most vigorously in spring and summer.

In the stagnant portion of the Zegrzyński Reservoir where the reproduction of *V. viviparus* is comparable to that in lake Białe, seston concentration can change significantly over a short period of time as a result of enhanced sedimentation and a decline in water flow velocity (Kajak, 1990). Such variable habitat conditions can decrease the availability or digestibility of food which is reflected in lower fertility. Connection with the Bug River caused less stable habitat conditions for viviparids dwelling in nearby oxbow lakes. Since snails feed mainly on organic matter, intensive feeding is the result of increased organic matter content. The sedimentation rate in oxbow lakes connected to the river was higher in spring than in autumn due to flooding and enhanced delivery of riverine organic matter (Porębski, 2006). However, the organic matter content in these habitats was smaller than in the isolated oxbow lakes. This accounts for intensive feeding in the beginning of the vegetation season when snails took advantage of larger concentrations of organic matter. In summer and autumn they then switched to algal food which had previously been scarce due to its outwashing by retreating river waters. Spring flooding in the Bug river usually take place in March and April and water retreat occurs at the beginning of June.

Size classes were similarly distributed in all habitats where the youngest snails were most numerous in spring, and the proportion of medium size and largest viviparids increased in summer and autumn. Fertility increased with shell height in all habitats except in the through-flow lakes. The statistically significant correlation coefficient confirmed that larger (older) viviparids had more embryos and this agrees with literature data. Buckley (1986) found that the age of the *V. georgianus* female indicates the size of its progeny and the future survival of young, as was also observed by Ribi and Gebhard (1986) in *V. ater*.

In the through-flow oxbow lakes, the most fertile females were in the II and III size classes. According to Calow (1978), semelparous species risk the loss of many young and iteroparous species refrain from reproduction under unfavourable environmental conditions. The unstable habitat of through-flow oxbow lakes forced earlier reproduction in *V. viviparus*, thus exibiting one expected animal strategic response to varying environmental conditions. This conclusion was confirmed by field experiments aimed at establishing the age of viviparids, where snails maintained in the habitat of through-flow water body grew faster and attained earlier maturity (Jakubik, 2007).

The studied oxbow lakes are astatic water bodies. In spite of similar origin, size, depth and initial water quality they are now characterized by more advanced limnological identity following large and irregular variability. They are mainly situated in agricultural catchments where the water quality and the composition of the lake bed sediments are affected by the imposed hydrological regime.The Szumin and Wywłoka oxbow lakes are connected to the Bug River and they are flooded by Spring river water. Subsiding waters then return part of the introduced matter back to the river channel.

The behaviour of iteroparous parents guarantees further reproduction even when environmental conditions tend to decrease it. Calow (1978) reported that iteroparous snails, and particularly prosobranch snails, have the tendency to inhabit small enclosed freshwater bodies. These conditions force snails to compete for limited resources and this is most likely the reason that only the fittest individuals grow and survive.

Such reproductive plasticity is a response to environmental variability, and here, these species have adopted special life strategies to combat unstable habitats. The semelparous, prosobranch freshwater snail *Bithynia graeca* which lives in the Kerkini artificial lake in northern Greece where water depth and volume rapidly changes, serves as another example (Eleutheiadis, Lazaridou-Dimitriadou, 1995). *B. graeca* adapted to water level fluctuations through a high net reproduction coefficient and by a high growth rate. A short life cycle, high productivity and investment of energy in reproduction together with rapid growth enabled *B. graeca* to succeed under the specific conditions of lake Kerkini. Early reproduction of *V. viviparus* from oxbow lakes is the response to periodical water rising in the river. The literature of Czarnołęski, Kozłowski, (1998); Czarnołęski et al., (2003) and Kozłowski & Teriokhin (1999), reports that the allocation of energy into early reproduction may be correlated with a shorter life span and therefore increased mortality. These observations therefore demand a detailed analysis of mortality in *V. viviparus* in the unstable habitat of oxbow lakes.

The research data here suggests that reproduction is the most important factor in the development of viviparid populations. This is essentially associated with the viviparity of these snails which enables them to control their reproduction processes and to promote the plastic life history trait in populations of *V. viviparus*.

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