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LIFE STRATEGIES OF VIVIPARIDAE (GASTROPODA: CAENOGASTROPODA: ARCHITAENIOGLOSSA) IN VARIOUS AQUATIC HABITATS: *VIVIPARUS VIVIPARUS* (LINNAEUS, 1758) AND *V. CONTECTUS* (MILLET, 1813)

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ABSTRACT: Viviparidae display two categories of life history traits – one constant and independent of habitat, another depending on ecological conditions. The relatively constant abundance is ensured by clustering in the same places at the same time, sex ratio (prevalence of females), size structure (presence of all size classes, with the largest snails forming the majority), and the high proportion of gravid females in the population. These traits undergo only seasonal variation in particular habitats. Adjustment to environmental changes involves the number of embryos per female and the size of reproducing females. Long-term life history studies were performed on *Viviparus viviparus* (L.) and *V. contectus* (Mill.) from various habitats (dam reservoir, river, oxbows connected to the river to varied extent) in Poland. The habitats differed in their surface area, depth and trophic status. The snails from the dam reservoir, ecotone zones in the river and stagnant oxbow lakes reproduced at a large body size, their fecundity being size-dependent. In very variable habitats, like oxbow lakes periodically joined to the river, viviparids reproduced at a younger age and smaller body size, while their fecundity did not increase with the body size. The reproduction was the most important factor determining the viviparid density in the studied habitats. This was mainly associated with the ovoviviparity which allowed for controlling the reproduction process. Reproduction is a flexible life history trait in the populations of *V. viviparus* and *V. contectus*.

KEY WORDS: Viviparidae, life strategies, size structure, fecundity, dam reservoir, oxbow lakes, river

INTRODUCTION

Life strategies are known to depend on habitat conditions (KOZŁOWSKI 1992, STEARNS 1992, JOKELA 1997). The main components of life history are body size, maximum physiological life span, growth rate, age at maturity, size and number of offspring, semelparity versus iteroparity (KOZŁOWSKI 1999). Some organisms stop growing having reached the optimum (considering all gains and losses) body size, and start reproducing (WEINER 1999). They usually produce numerous offspring, many of which die before attaining maturity. Such a life strategy is characteristic of annual organisms which start reproducing soon after growth completion (KOZŁOWSKI et al. 2004).

In some perennial organisms the growth is indeterminate and continues after attaining maturity but at a rate decreasing with age (KOZŁOWSKI 1996, CZARNOŁĘSKI & KOZŁOWSKI 1998). Such growth is characteristic of ectothermic vertebrates like fishes, amphibians and reptiles and, among invertebrates, of some molluscs and most annelids (e. g. CZARNOŁĘSKI et al. 2003, 2005). In such species the growth is the fastest short before or short after reaching maturity (e.g. FROESE & PAULY 2005).

Each of these two strategies requires many adaptations, some expressed already at the embryonic stage. In placental mammals the embryos develop inside the mother's organism which limits the mortality among the offspring. The situation is similar in birds, particularly in nidifugous species. In ovoviviparous molluscs the embryonic development taking place inside the

parent's organism implies a markedly greater chance of survival for the young which are born with developed shells. Variable habitats enforce development of life strategies which are optimum in given conditions (REZNICK et al. 1990).

Since the classic paper by COLE (1954), who emphasised the importance of life cycles, many papers have been published, describing the functioning of freshwater mollusc populations under different habitat conditions (e.g. RUSSELL-HUNTER 1961a, b, CALOW 1978, EVERSOLE 1978, DILLON 2000). These issues are most often revealed when studying the ecological and evolutionary importance of fecundity or reproductive effort (EVERSOLE 1974, BROWNE & RUSSELL-HUNTER 1978, ALDRIDGE 1982, BUCKLEY 1986, CAQUET 1993, VELECKÁ & JÜTTNER 2000, VELECKÁ et al. 1998, GLAUBRECHT 2006, NORTON & BRONSON 2006).

Most terrestrial and marine gastropods are iteroparous, relatively long-lived organisms, while most freshwater snails, particularly pulmonates, are semelparous, with the life span of one year (Fig. 1). The evolution of semelparity in fresh waters is probably a response to harsh and unstable conditions of these waters, due to low osmotic pressure and fluctuations of physical and chemical properties which is associated with the land impact. Freshwater ecosystems are subject to influx of toxic and biogenic substances from the surrounding land. Hence, freshwater ecosystems are quite variable and it is possible that frequent fluctuations of water level, or sometimes even disappearance of small water bodies, have enforced the strategy of investing energy in the offspring at the expense of parental individuals.

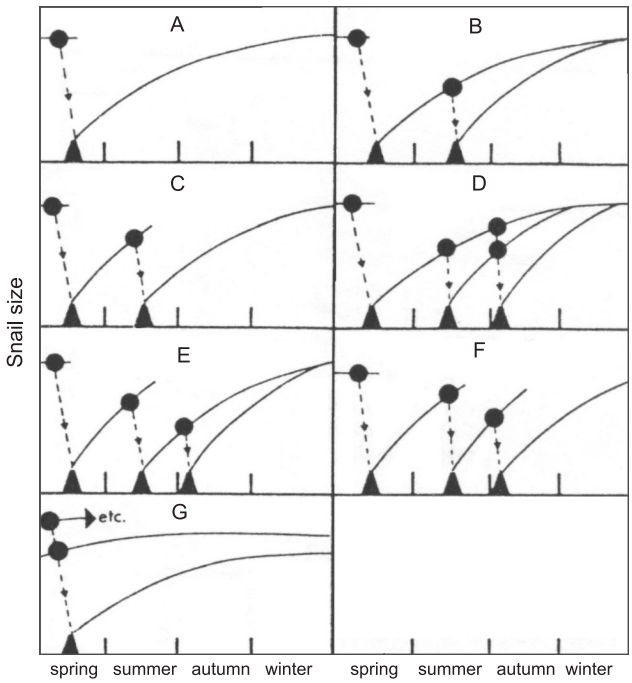

Fig. 1. Life cycle patterns in freshwater snails (A–G); circles – beginning of reproduction, triangles – appearance of egg capsules (after CALOW 1978)

The annual cycle with the reproduction in the spring and total replacement of one generation by another (type A) prevails among the freshwater pulmonates (CALOW 1978). Life cycles with the summer (types B and C) or autumn (types D, E and F) reproduction and total generation replacement are also common. In different habitats these life cycles may replace each other, for example in fertile habitats type A may transform into types B, C or D (BROWN 1985a, b, CAQUET 1993).

Most prosobranch snails (Caenogastropoda) display G type life cycles. These are exclusively iteroparous species. Some iteroparous species, however, show other life cycle patterns, for example type A has been found in *Valvata piscinalis* (FRETTER & GRAHAM 1978, GRIGOROVICH et al. 2005).

Iteroparity guarantees further reproduction in case of failure, and allows for repeated multiplying of the parent's genes. It is frequent in species like *Viviparus contectus* or *Bithynia leachii* which often live in isolated freshwater reservoirs. Under such conditions, competition for food and space is higher, and the survival of parent individuals increases the chance of survival of the population.

Most freshwater Caenogastropoda are dioecious and hermaphroditism is rare, however it prevails among pulmonates (HELLER 2008). It increases the chance of meeting a partner; this is of particular importance at a low density of snails during the reproductive period in semelparous populations.

Oviparity is the most common mode of reproduction in both terrestrial and aquatic gastropods. The development of fertilised eggs takes place inside the egg envelopes outside the parent's organism. Bar a few exceptions, in terrestrial snails parental care does not extend beyond egg lying. Marine Caenogastropoda, on the other hand, have developed an array of ways of protecting their eggs from adverse environmental conditions. Water level fluctuations, temperature changes and seasonal variation in many factors have resulted in differences in the number of eggs, egg morphology, mode of egg laying and attaching eggs to the substratum among freshwater snails (FALNIOWSKI 2001, KIRKEGAARD 2006).

Most freshwater Caenogastropoda are oviparous. They lay eggs in the form of cocoons attached to the substratum. A single individual develops in each egg capsule, or the capsule may contain from several to several dozen eggs. From such a great number of eggs, only one may hatch while the others serve as food for the developing embryo, as is the case in *Theodoxus fluviatilis*.

Many gastropods, both terrestrial (Stylommatophora) and aquatic (*Littorina saxatilis*, *Planaxis sulcatus*, Viviparidae, *Potamopyrgus antipodarum*), are ovoviviparous. In these snails fertilised eggs develop

inside the oviduct or spermoviduct which is their exclusive protection.

The native freshwater Caenogastropoda are mainly oviparous, except for three species: *Viviparus viviparus*, *V. contectus*, and *Valvata naticina*. *Potamopyrgus antipodarum* from New Zealand – an invasive species in Poland – is also ovoviviparous.

In *Viviparus* and *P. antipodarum* embryos develop in capsules kept in the mother's uterus. Ovoviviparity provides protection for the developing young. Therefore, its success often depends on the survival probability of the parent during reproduction. Rare cases of true viviparity – development of embryos inside the parent's organism from which they acquire nutritive substances – has been reported in some terrestrial Stylommatophora (HELLER 2001).

Freshwater Viviparidae are a typical iteroparous and ovoviviparous family. Their present distribution range covers all continents except South America where they are found only as fossils (FALNIOWSKI 1989a, b, FALNIOWSKI et al. 1996a, b, c, 1997, 1998). In Europe Viviparidae are represented by four species: *V. acerosus* (Bourguignat, 1862), *V. ater* (De Cristofori et Jan, 1832), *V. contectus* (Millet, 1813) and *V. viviparus* (Linnaeus, 1758) (FALKNER et al. 2001). *V. contectus* and *V. viviparus* occur in freshwater habitats of Poland.

V. viviparus lives in large rivers, oxbows and – less frequently – in lakes and heavily overgrown ponds. It prefers sandy, loamy, muddy or stony bottom. It is practically absent from seasonal water bodies and small overgrowing stagnant waters (e.g. RIEDEL 1954, DROZDOWSKI 1979). Its distribution range extends to the Urals, Sweden, France and eastern part of Great Britain (FALNIOWSKI 1989a). In Poland the species is common in the lowlands of the northern and central part of the country (sporadically on the Baltic coast). It is sometimes found in southern Poland, among others in anthropogenic water bodies of Silesia (STRZELEC 1993).

V. contectus prefers heavily silted and shallow stagnant water bodies – oxbow lakes, flooded meadows, ponds, peat excavations or boggy reservoirs. It also inhabits slow-flowing, small rivers and lacustrine rush zones (ZHADIN 1952). The species is associated with muddy bottom covered by a thin layer of detritus and with partly vegetated places (PIECHOCKI 1969). It inhabits waters of almost entire Europe and western Siberia (ZHADIN 1952) with the exception of the Balkan and Apenninic peninsulas and the western part of the British Isles. In Poland *V. contectus* is found in waters all over the country except for the Carpathians and the Sudetes.

Both species inhabit seasonal water bodies where the availability of resources undergoes regular seasonal variation. The duration of seasons may vary and thus affect life history traits in the populations. The diversity of sites inhabited by Viviparidae is matched by flexible physiological processes which evidently decide upon adjustment of the snails to such conditions. The sex ratio and size (age) structure, as well as the proportion of gravid females, are important for maintaining the viviparids' density in such seasonal habitats. The flexible components of life strategies of Viviparidae are the age at maturity and the number of offspring per female. The adjustment to environmental changes is possible due to iteroparity, dioecism and ovoviviparity.

Viviparid embryos develop within the egg capsules (FRETTER & GRAHAM 1978). In the mother's brood chamber the embryos are arranged according to the advancement of their development. The oldest embryos – juveniles with developed shells – are in the outlet part of the chamber. They are enveloped by the egg capsule which breaks before or after birth (ALAKRINSKAYA 1969).

Analysis of the literature data presented above raises the question of how the viviparid life strategies are differentiated and what factors determine them. This is the main issue of this paper. The study is an attempt to answer the following questions: 1. does the life strategy of Viviparidae function in an unchanged form? 2. which traits of viviparid life history are habitat-dependent and which are not? 3. how do viviparids benefit from their viviparity and iteroparity?

Some of these problems have been partly addressed in earlier papers (JAKUBIK 2000, 2003, 2006, 2007, 2009a, b, JAKUBIK & AUGUSTYNIUK 2002, JAKUBIK & LEWANDOWSKI 2007, JAKUBIK & STAŃCZYKOWSKA 1996, JAKUBIK et al. 2006, 2007). In this paper these issues are comprehensively re-analysed and supplemented with unpublished materials.

STUDY AREA

Snails of the family Viviparidae are common in the lowlands of northern and central parts of Poland. Due to earlier analyses of viviparids' adaptations to various habitat conditions, study sites of different origin, size, depth and hydrological regime could be selected. The studies were carried out in a dam reservoir (Zegrzyński Reservoir, central Poland), ecotone habitats – outlet sections of the Bug, Narew and Rządza rivers discharging to the reservoir, in the Narew River (between 82 and 170 km of its course) and in oxbow lakes of the Bug River, either periodically flooded or totally isolated from the river (Fig. 2).

The Zegrzyński Reservoir was built in 1962 by damming of the Bug and Narew rivers. The planned

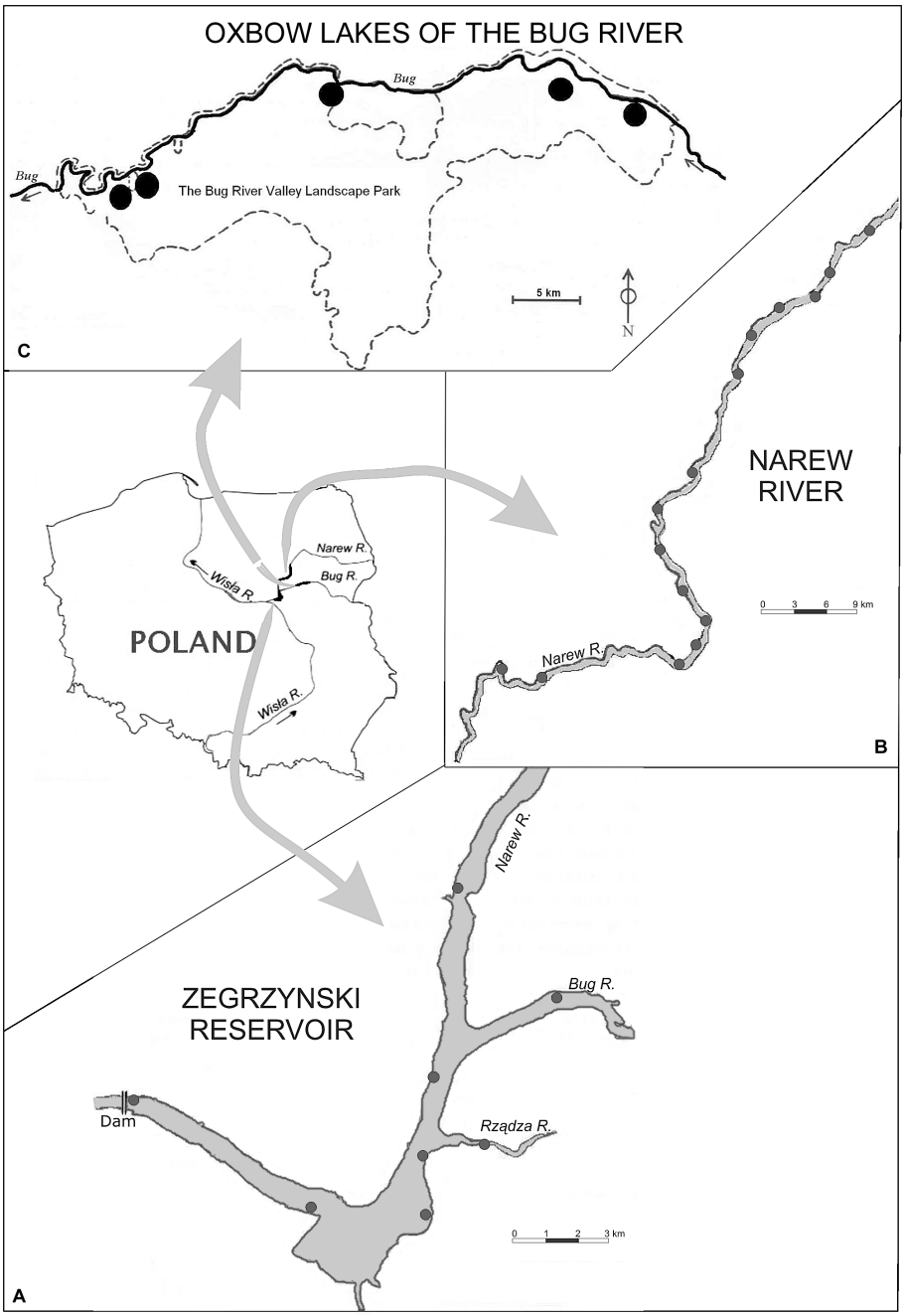

Fig. 2. Study area and location of sampling sites (A – Zegrzyński Reservoir, river outlets, B – Narew River, C – Bug River, oxbow lakes)

water level was achieved in the spring of 1964. Apart from energetic, flood control and transport purposes, the reservoir is a recreational area and a source of drinking water for Warsaw. Its main morphometric parameters are shown in Table 1. Detailed characteristics of the Zegrzyński Reservoir has been presented in KAJAK (1990, 1991), KAJAK & DUSOGE (1989), OLSZEWSKI & MÓWIŃSKA (1985), WOJTKOWSKA (1997) and JAKUBIK (2003).

The Zegrzyński Reservoir is fed by the rivers Narew (42% of water), Bug (58%) and Rządza (less than 1%). The Narew River carries off-class water (over 19.2%), or meets the requirements of the 3rd quality class (80.8%) (NATURE PROTECTION 2000). According to

Table 1. Basic morphometric parameters of the Zegrzyński Reservoir (after KAJAK 1990, modified)

Surface area [km^2]		Catchment/reservoir area ratio	Length [km]	Width [km]	Capacity [mln m^3]		Depth [m]	
catchment	reservoir				total	effective	mean	maximum
103.6	33.0	3.0	60	0.5–3.0	100.0	0.5–11.0	3.5	9.0

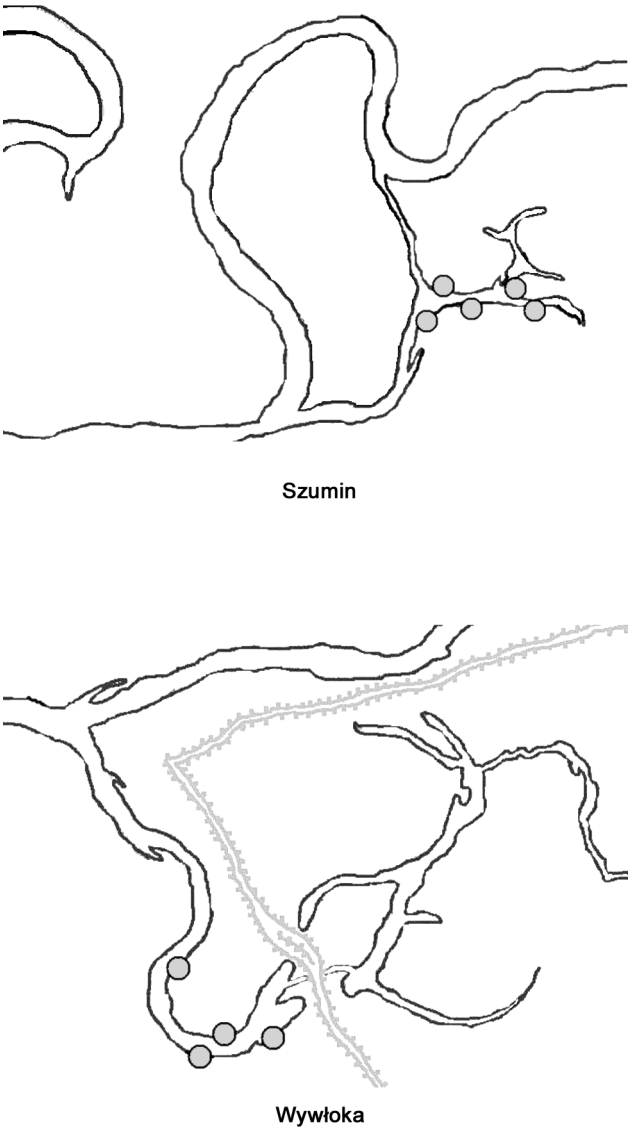

Fig. 3. Details on location of sampling sites – flow oxbows (Bug River)

NATURE PROTECTION (2000), the Bug River is even more polluted than the Narew River, with 79.0 % of off-class water, and 21.0 % of the 3rd class quality water. The Narew and Bug rivers are polluted with a great amount of communal waste from the towns and resorts situated along their course. The Rządza River, the third tributary of the reservoir, is about 60 km long, with the average water flow (1994) of 21 m^3/s (FALKOWSKI 1995), and off-class water (REPORT... 2002, 2008).

The studies included five oxbow lakes of the Bug River, all situated in the Nadbużański Landscape Park. The river meanders and forms numerous oxbows there. The selected oxbows are connected with the river to a different extent – from periodically connected with the river (Szumin and Wywłoka) (Fig. 3) to permanently isolated from the river course (Wszebory, Lake Białe, Bużysko) (Fig. 4).

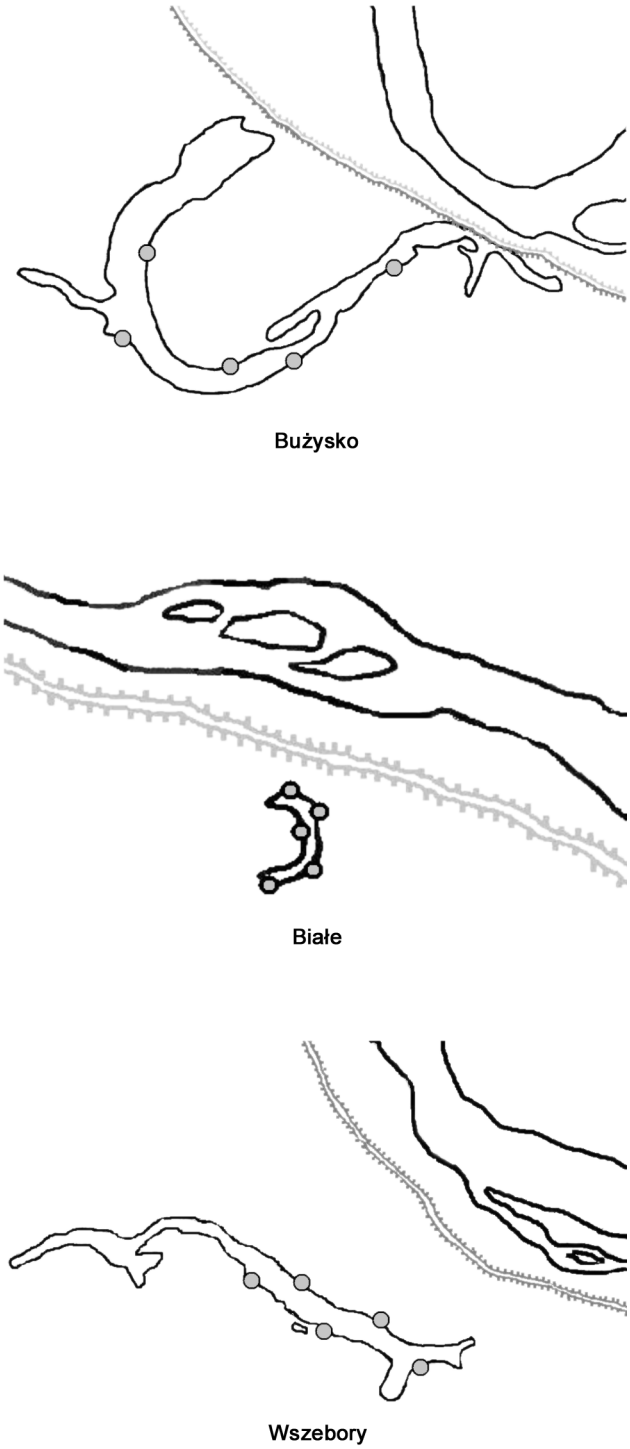

Fig. 4. Details on location of sampling sites – isolated oxbows (Bug River)

Oxbow lake Szumin has the area of 17.0 ha and maximum depth of ca. 4 m. Its connection with the river was made in the 1970s, and a natural escarpment was used to build flood embankment in the 1980s. Recently, the river has found a new connection to this lake. Land use in the catchment area is of a mixed

structure. The southern shore is built up with a holiday estate.

Oxbow lake Wywłoka has the area of 23.4 ha and maximum depth of ca. 3 m. In the 1980s it was cut with a dike equipped with culverts. The western arm of the oxbow opens to the Bug River. The lake is fed by the Ugoszcz River. Its catchment area is dominated by meadows and pastures with small thickets. There is a holiday estate on the southern shore. The lake is joined to the Bug River during high water flows through a sluice built in the embankment.

Oxbow lake Wszebory has an area of 11.7 ha and maximum depth of c. 4 m. Its catchment basin is flat. A group of summer cottages closely surrounds one end of the lake. On the opposite shore there are some remnants of an old bank reinforcement. At high water levels the lake is connected with the Bug River through an embankment sluice.

Lake Białe, totally isolated from the Bug, has the area of 1.5 ha and maximum depth of 4 m. It is probably the oldest oxbow lake in the lower section of the river. The lake is situated at the edge of a meadow and surrounded by trees and shrubs.

Oxbow lake Bużysko near the village Morzyczyn Włościański is also isolated from the river. Its surface area is 16.2 ha and its maximum depth – ca. 2.5 m. The lake was separated from the main river channel by flood embankments built in 1976. Most (80%) of its catchment area is covered by extensively used meadows and pastures for cattle and horses. Ca. 2/3 of the lake area is overgrown by the water soldier.

MATERIAL AND METHODS

The studies in the Zegrzyński Reservoir and in the outlet sections of the Bug, Narew and Rządza rivers were carried out in 1995–2008 and those in the oxbow lakes of the Bug River – between 2003 and 2008. Out of the 48 selected sites, five were situated in the Zegrzyński Reservoir, three in the outlet river sections, 15 in the Narew River, and 25 in the oxbow lakes of the Bug River (5 sites in each lake – Figs 2–4).

Molluscs were sampled in the near-shore zone in the spring (April, May), summer (June-August) and autumn (September, October). Depending on the depth, different sampling methods were used. To the depth of 1 m, snails were collected with the Ekman dredge. At deeper sites samples were taken with a bottom dredge (side size 40 cm) which was dragged along 1 m, parallel to the shore. The collected material was washed on a sieve of the mesh size of 1 mm which allowed for obtaining viviparids of all size classes.

The sex of snails was determined based on morphological differences: the right tentacle of males is thicker and serves as the copulatory organ; in females both tentacles are of the same thickness (PIECHOCKI 1979). Besides, empty shells and dead viviparids (i.e. shells with decomposing snail's body or its remnants) were collected in the oxbow lakes of the Bug River.

To estimate the size structure of live and dead individuals and empty shells, shell height and width were measured with the accuracy of 0.1 mm. The measurements made it possible to analyse the collected material according to a four-grade scale of sizes, adopted earlier by STAŃCZYKOWSKA (1960a): class I – shells of a height and width from 5.0 to 8.0 mm, covered by characteristic hairs, II – shell height and width of 8.1–12.0 mm, III – shell height 12.1–25.0 mm, shell width 12.1–20.0 mm, IV – shell height > 25.0 mm, shell width > 20.0 mm.

Females of *V. viviparus* were dissected to distinguish these with embryos in the brood chamber (uterus) and those without embryos, and to determine their fecundity. The embryos were removed from the brood chambers, counted and measured. This procedure allowed for determining the indirect index of females' reproductive effort (IEI) according to CALOW (1978):

$$IEI = (E \times EV)/SV,$$

where: E – number of eggs produced during the reproduction season, EV – egg volume (calculated as $4/3\ \Pi\ r^3$, assuming spherical shape), SV – parent's volume (calculated as $4/3\ \Pi\ r^2h$, assuming conical shape), r – egg or shell radius, h – shell height.

According to the development advancement, the embryos were divided into three groups: a – the youngest – translucent egg capsules in the upper part of the brood chamber, b – medium-advanced – egg capsules with visible shell outlines in the middle part of the brood chamber, c – the oldest – fully developed embryos with shell, sometimes surrounded by protein coating and situated in the outlet part of the brood chamber.

Viviparids from the oxbow lakes were analysed for the presence of trematode larvae, according to the methods given in JEŻEWSKI (2004). The trematode species were identified based on morphological characters, using POJMAŃSKA's (1971, 1972) keys.

Physical and chemical characteristics of the studied sites were supplemented with the analyses of water sampled in the spring, summer and autumn of 2007–2008. Dissolved oxygen (measured with the WTW Oxi340i probe) and pH (measured potentiometrically) were determined in the field. Water for chemical analyses was taken with the Patalas sampler of the volume of 2.5 dm^3 in three replicates.

Concentration of calcium ions was determined by complexometric titration (HERMANOWICZ et al. 1999). Ammonium nitrogen was determined with the indophenyl blue method (SOLÓRZANO 1969), and soluble reactive phosphorus was analysed with the molybdenum blue method using stannous chloride as the reducing agent.

Bottom sediments were sampled with the tubular sampler of 47 mm diameter in three replicates, dried at room temperature for several days and sieved through a sieve of 1 mm mesh size. Following sieving, the samples were dried at 105°C to constant weight. Subsamples of bottom sediments were pulverised, weighed and combusted in a muffle furnace at 530°C for ca. 6 hours. After combustion, the crucibles were cooled in a dessicator and weighed. Percent content of organic matter was calculated from the difference between the sediment mass before and after combustion.

To determine the content of total nitrogen and phosphorus, dried and sieved bottom sediments were mineralised in a mixture of concentrated sulphuric acid and 30% hydrogen peroxide. In the resulting solutions, nitrogen and phosphorus were determined with the methods described above (STANDARD METHODS 1999).

ANOVA and χ^2 test were used to check the differences between the compared parameters. Since the tests did not reveal differences between the sites and consecutive study years in particular habitats, the results were presented in the form of means. Due to the lack of significant differences, the outlet sections of the studied rivers were treated jointly as the same habitat. The same was true of the flow oxbows on the one hand and the isolated oxbows on the other. Differences in the mean number of embryos, in the reproductive effort and season were tested with the Newman-Keuls and Tukey tests. The Pearson correlation was used to describe the relationship between the growth stages of the embryos and the degree of parasite infection. Comparison of the sex ratio, proportion of gravid and non-gravid females and percentage of females in size classes was done with the G test. Multifactor GLM analysis considering quantitative and qualitative factors was used to determine the effect of habitat, season and snail size on the fecundity (mean number of embryos per female).

RESULTS

CHEMICAL CHARACTERISTICS OF THE STUDIED HABITATS

Chemical parameters of the studied sites are presented in Table 2. Water pH ranged from 6.1 to 9.1 and was lower in the Zegrzyński Reservoir than in the other habitats (Table 2). Analyses of dissolved oxygen showed good aeration of the studied habitats, though the range of recorded concentrations was wide in the oxbow lakes, both isolated and connected with the river. The analysed waters were soft. Calcium concentration in all the studied habitats was low, ranging from 60.1 to 79.1 mg dm^{-3} and classified the waters to the 2nd quality class. Concentrations of organic matter, phosphorus and nitrogen in the water and bottom sediments varied. The mean concentration of dissolved nitrogen ranged between 0.01 and 7.56 mg dm^{-3}. The greatest concentrations of dissolved nitrogen were found in the oxbow lakes (to 7.56 mg dm^{-3}) and outlet sections of the rivers (3.60 to 6.15 mg dm^{-3}). Concentration of dissolved phosphorus varied between 0.048 and 1,517 mg dm^{-3}. The sites varied widely in the concentration of dissolved phosphorus which was higher in the oxbow lakes. The highest concentrations of phosphorus were noted in the oxbow lake Bużysko (155 to 1,517 mg dm^{-3}). Such high phosphorus content in this isolated lake was a result of surface runoff from the surrounding land. The mean concentration of organic matter in the bottom sediments varied between 0.97 and 57.08% dry weight. Sediments of the Narew River were the richest in organic matter (37.8% dry weight), particularly in its outlet section (57.08% dry weight). From among the studied oxbow lakes, the sediments of Lake Białe had the greatest content of organic matter (24.37% dry weight). In the other oxbow lakes the sediment content of organic matter ranged from 1.77 to 12.77% dry weight. The mean concentration of total phosphorus in the bottom sediments varied between 0.13 and 1.22 mg g^{-1} dry weight, the latter value was noted in the sediments of the Narew River. In the oxbow lakes the mean concentration of total phosphorus was 0.13–0.46 mg g^{-1} dry weight. A higher phosphorus content was noted in the isolated oxbow lakes – the highest in the sediments of lake Wszebory (0.46 mg g^{-1} dry weight). Concentrations of phosphorus in the bottom sediments of the oxbow lakes were within the range noted in other water bodies, for example in shallow lakes of Florida (OLILA & REEDDY 1993), in English (CLARKE & WHARTON 2001) and some Canadian (CHAMBERS & PREPAS 1990) lakes. The mean concentration of total nitrogen varied between 0.77 and 60.30 mg g^{-1} dry weight of the sediment. The lowest nitrogen content was found in the Zegrzyński Reservoir (0.77 mg g^{-1} dry weight) and the highest – in the isolated oxbow lakes (60.30 mg g^{-1} dry weight in the sediments of Lake Białe and 51.34 mg g^{-1} dry weight in those from Bużysko). These values were

Table 2. Chemical characteristics of the studied habitats (according to KAJAK 1990, JAKUBIK et al. 2006, 2007, REPORT, 2002, 2008, STRZAŁEK 2006, own unpublished)

Habitat		pH	O_2 [mg·dm^{-3}]	Ca [mg·dm^{-3}]	N total [mg dm^{-3}]	P total [mg dm^{-3}]	Organic matter [% dry weight]	P [mg g^{1} dry weight]	N [mg g^{-1} dry weight]
				water			bottom sediments		
Zegrzyński Reservoir		6.1–6.4	8.7 8.2–9.4	76.6–78.8	3.90–5.15	0.053–0.146	0.97±0.60	0.20±0.11	0.77±0.25
River outlets	Bug	7.5–9.1	9.1 6.2–12.9	72.1–73.7	4.06–5.48	0.079–0.166	2.41±0.18	0.22±0.02	3.02±0.82
	Narew	7.4–8.8	9.3 6.2–11.5	68.9–72.1	3.60–6.15	0.052–0.096	57.08±13.04	0.99±0.30	12.14±7.41
	Rządza	7.5–8.7	8.5 6.1–12.1	64.8–66.3	3.98–6.12	0.048–0.087	18.6±2.19	0.32±0.09	6.08±1.67
Narew River		7.8–9.0	9.5 8.1–10.2	73.1–77.3	0.01–0.53	0.175–0.950	37.8±12.30	1.22±0.39	15±8.13
Oxbows connected to the Bug River	Szumin	6.7–8.5	10.7 9.8–11.6	61.7–78.6	0.43–3.97	89–229	3.33±3.48	0.13±0.14	4.74±6.08
	Wywłoka	6.8–7.3	5.8 4.0–8.6	60.1–75.4	0.23–3.51	26–122	1.77±1.76	0.15±0.15	4.05±3.98
Isolated oxbows connected to the Bug River	Wszebory	6.7–8.1	5.1 4.5–5.7	72.1–79.3	0.29–7.39	42–132	4.08±6.62	0.46±0.97	14.95±12.38
	Jezioro Białe	6.5–7.4	6.9 3.9–6.0	74.5–78.5	0.30–7.56	23–146	24.37±19.36	0.35±0.18	60.30±36.80
	Bużysko	6.7–8.0	7.4 0.2–8.8	72.3–79.1	0.07–2.76	155–1,517	12.77±9.91	0.32±0.24	51.34±45.31

For O_2 mean values and ranges (below) are given; for organic matter, P and N – mean values ± S.D.; other parameters are presented as ranges

several times higher than those cited in the literature (KAJAK & ŁAWACZ 1977, CHAMBERS & PREPAS 1990, LIGĘZA et al. 2007).

DENSITY AND BIOMASS

Viviparidae inhabited the near-shore zone of the studied habitats: the dam reservoir, outlet sections of the Bug, Narew and Rządza rivers, the Narew River and the oxbow lakes of the Bug. The changes in the density and biomass in particular sites were similar and did not show statistically significant differences (df=17, χ^2=8.43, p<0.90; df=17, χ^2=18.25, p<0.90; df=5, χ^2=18.13, p<0.90; df=5, χ^2=13.25, p<0.90). Differences were found only between the habitat types. The density and biomass of *V. viviparus* varied according to habitat and season. *V. contectus* was found only sporadically in the Zegrzyński Reservoir, in the outlet river sections and in the Narew River. It occurred at higher densities in the flow and isolated oxbow lakes. Therefore, the population model of *V. contectus* presented here is based on data from the latter habitats.

Density and biomass of *V. viviparus*

Mass occurrence of *V. viviparus* was observed in the earlier studies (1990–1995) in the near-shore zone of the Zegrzyński Reservoir and in the river outlets (JAKUBIK 2003). The summer viviparid densities in the reservoir reached 500 ind. m^{-2}, in the river outlets they exceeded 500 ind. m^{-2} and in the lower section of the Narew more than 800 ind. m^{-2} were observed.

The density of *V. viviparus* differed among the sites (ANOVA, p<0.05) in consecutive years. The greatest densities were recorded in the Narew and in the river outlets (500 ind. m^{-2} on average); they were smaller in the dam reservoir (265 ind. m^{-2}) and the smallest – in the flow (150 ind. m^{-2}) and isolated (120 ind. m^{-2}) oxbow lakes (Tukey test, p<0.05) (Fig. 5A). The densities did not differ significantly between the two types of oxbow lakes (Tukey test, p=0.56).

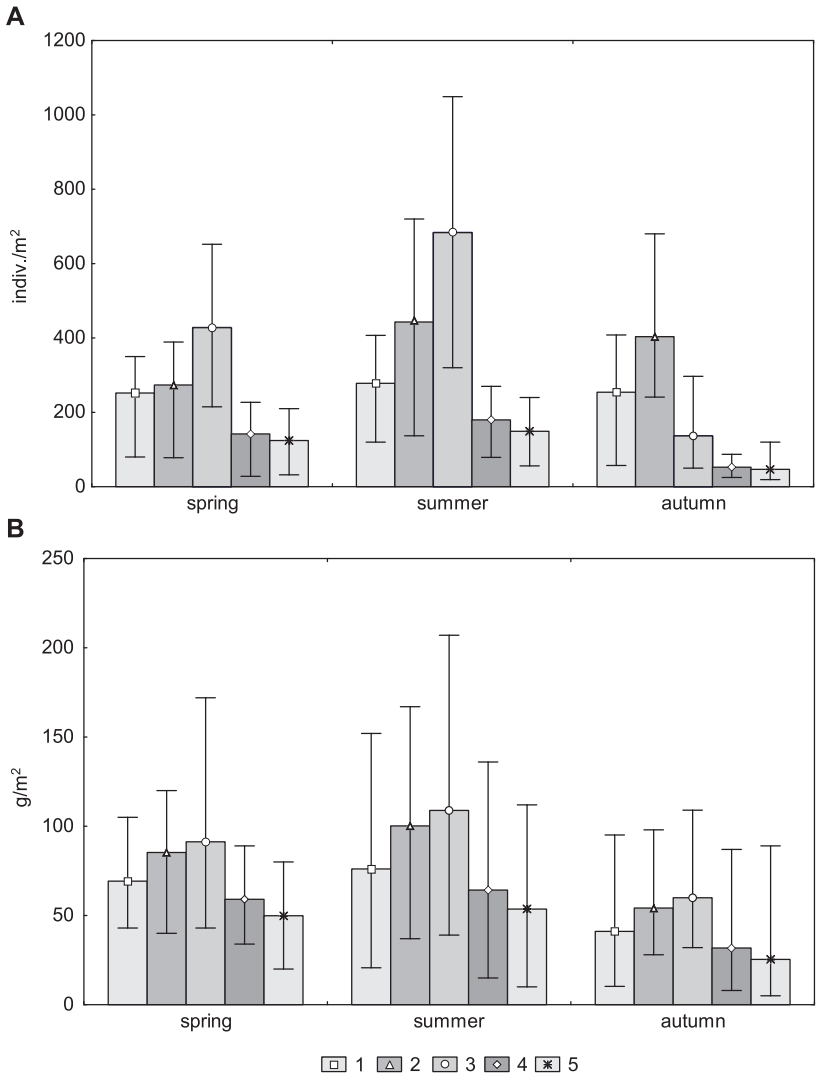

Fig. 5. Seasonal changes in abundance (A) and biomass (B) of *V. viviparus* in different habitats: 1 – Zegrzyński Reservoir, 2 – river outlets, 3 – Narew River, 4 – flow oxbows, 5 – isolated oxbows; mean values of 1995–2008 (1–3) and 2003–2008 (4–5) with max – min ranges

The mean snail biomass (dry body weight with shell) differed among the habitat types (ANOVA, $p<0.05$) (Fig. 5B), as did the density. The highest biomass was found in the river (92 g m^{-2} on average) and in the outlet sections (85 gm^{-2}); the values were smaller in the reservoir (66 gm^{-2}), flow (55 gm^{-2}) and isolated (45 gm^{-2}) oxbow lakes (Tukey test, $p<0.05$).

Populations of *V. viviparus* occurred in aggregations which were recorded in the same places in consecutive years. Variance analysis showed the effect of season on the density and biomass of the aggregation-forming viviparids. Statistically significant differences were found between the spring and summer aggregations (df=15,815, $p<0.001$), the summer and autumn aggregations (df=15,397, $p<0.001$) and between the spring and autumn aggregations (df=15,245, $p<0.001$). The relatively low density and biomass of the spring population of *V. viviparus* increased to achieve their maximum in the summer and decrease subsequently.

Density and biomass of *V. contectus*

Habitat and season were found to influence the density of *V. contectus* (ANOVA, $p<0.05$). The snails were sporadically found in the Zegrzyński Reservoir (mean 3 ind. m^{-2}), in the river outlets (5 ind. m^{-2}) and in the Narew River (8 ind. m^{-2}) where they did not form aggregations. *V. contectus* from the oxbow lakes formed, however, aggregations in the same places every year. They accompanied the aggregations of *V. viviparus*. The densities of *V. contectus* were similar in both types of oxbow lakes (Tukey test, $p=0.515$) amounting to 23 ind. m^{-2} on average, with the maximum density of 30 ind. m^{-2}. The highest densities, noted in the spring and summer, did not differ between the two types of oxbows (Tukey test, $p=0.801$, $p=0.981$) (Fig. 6A). In the autumn the densities decreased significantly (Tukey test, $p<0.001$).

The snail biomass differed between the two types of oxbows (t-test, $p<0.001$). The mean biomass of *V. contectus* was 47 g m^{-2} in the flow lakes and 39 g m^{-2} in the isolated lakes (Fig. 6B). ANOVA showed a significant effect of season on the biomass of *V. contectus* in both types of oxbow lakes ($p<0.05$) (Fig. 6B). The largest biomass was recorded in the summer, slightly smaller – in the spring and the smallest – in the autumn. Statistically significant differences in the biomass were found between the spring and summer (df=5,113, $p<0.001$), the summer and autumn (df=5,900, $p<0.001$) and between the spring and autumn (df=5,400, $p<0.001$).

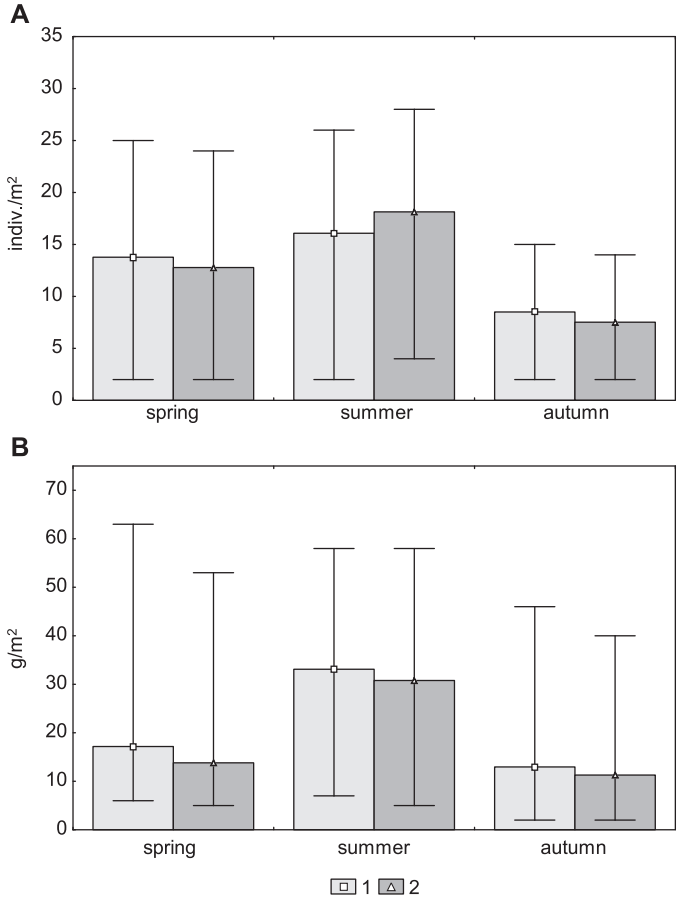

Fig. 6. Seasonal changes in abundance (A) and biomass (B) of *V. contectus* in: 1 – flow oxbows, 2 – isolated oxbows; mean values of 2003–2008 with max – min ranges

SIZE STRUCTURE

The size structure within the habitats did not differ statistically significantly among the years (df=17, χ^2=10.12, p>0.50; df=5, χ^2=17.12, p>0.50). It was compared among the habitats and seasons.

Size structure in *V. viviparus*

Snails of all size classes were found in the studied habitats; classes II, III and IV dominated in most sites. The proportion of the youngest (class I) snails was small (Fig. 7A). The size structure changed during the season (ANOVA, p<0.001) (Fig. 7A). Smaller snails (classes I and II) dominated in the studied populations in the spring, and larger (III and IV) – in the summer and autumn. This was particularly visible in the Narew River and in the river outlets where the proportion of class I snails was high in the spring (39% in the Narew and 15% in river outlets) (Tukey test, p<0.001) while classes III and IV contributed more to the total density in the summer and autumn (Tukey test, p<0.001).

Size structure of *V. contectus*

Snails of all size classes occurred in both types of oxbow lakes (Fig. 7B). Most of them represented classes II, III and IV. The proportion of the youngest individuals was small and amounted to ca. 10% of the population. Snails of class II dominated in the spring and autumn (Tukey test, p<0.05) and those of class III – in the summer (Tukey test, p<0.001).

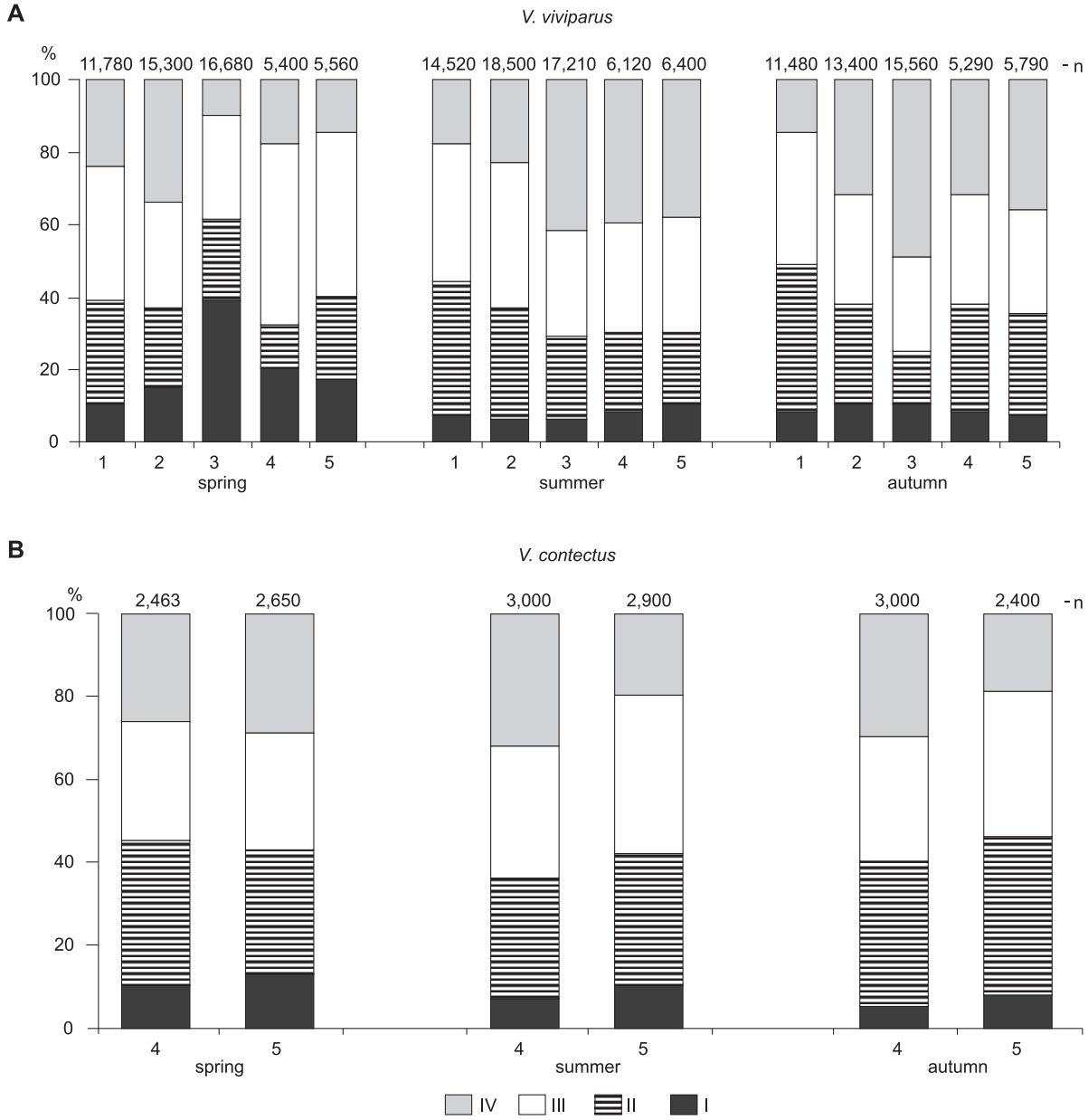

Fig. 7. Seasonal changes in the proportion of size classes (I–IV) of *V. viviparus* (A) and *V. contectus* (B) in different habitats: 1–5 see caption to Fig. 5; mean values of 1995–2008 (1–3) and 2003–2008 (4–5)

REPRODUCTION

Sex ratio of *V. viviparus*

Small, insignificant differences in the sex ratio noted in the material collected from all the habitats in the whole study period allowed for presenting them in the form of means for all habitat types (df=17, χ^2=9.34, p<0.90, df=5, χ^2=9.34, p<0.90).

In the studied populations the predominance of females or similar proportion of both sexes were observed (Table 3). The sex ratio changed during the vegetation season. The greatest proportion of females was noted in the summer (up to 82% in the river outlets), slightly smaller – in the spring (ca. 60%) and the smallest – in the autumn (up to 50% in the Zegrzyński Reservoir and river outlets). Statistically significant differences in the percentage of females were noted between the spring and autumn (G=7.60, p<0.005), between the summer and autumn (G=11.12, p<0.001) and no differences were found between the autumn and spring (G=3.90, p=0.127).

Sex ratio in *V. contectus*

The sex ratio in *V. contectus* from the studied sites was 1:1. No significant differences in this respect were found between the seasons (Table 4).

Table 3. Proportion [%] of female and male *V. viviparus* in spring, summer and autumn in the Zegrzyński Reservoir (1), outlet river sections (2), Narew River (3), flow oxbows (4), and isolated oxbow (5) (numbers of individuals given in parentheses)

Sex	Season	Habitat					G-test (df=3)
		1	2	3	4	5	
♀	spring	60	60	62	63	60	spring/summer
		(7,070)	(9,180)	(10,340)	(3,400)	(3,340)	7.60*
	summer	78	82	80	75	73	summer/autumn
		(11,330)	(15,170)	(13,360)	(4,050)	(4,060)	11.12**
	autumn	50	50	60	52	51	autumn/spring
		(5,740)	(6,700)	(9,340)	(2,750)	(2,950)	3.90, p=0.127
♂	spring	40	40	38	37	40	spring/summer
		(4,710)	(6,120)	(6,340)	(2,000)	(2,220)	7.70*
	summer	22	18	20	25	27	summer/autumn
		(3,190)	(3,330)	(3,850)	(2,070)	(2,340)	8.60**
	autumn	50	50	40	48	49	autumn/spring
		(5,740)	(6,700)	(6,220)	(2,540)	(2,840)	4.60, p=0.132

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

Table 4. Proportion [%] of female and male *V. contectus* in spring, summer and autumn in flow oxbows (4) and isolated oxbow (5) (numbers of individuals given in parentheses)

Sex	Season	Habitats		G-test (df=3)
		4	5	
♀	spring	54	48	spring/summer
		(1,303)	(1,280)	4.20, p=0.230
	summer	53	49	summer/autumn
		(1,530)	(1,440)	8.20, p=0.125
	autumn	47	46	autumn/spring
		(1,480)	(1,160)	2.30, p=0.024
♂	spring	46	52	spring/summer
		(1,160)	(1,370)	3.50, p=0.120
	summer	47	51	summer/autumn
		(1,470)	(1,460)	5.30, p=0.120
	autumn	53	54	autumn/spring
		(1,520)	(1,240)	3.50, p=0.215

Size structure of female and male *V. viviparus*

The analysis of size structure of female and male viviparids in consecutive years and in all the habitats did not show significant differences (df=17, χ^2=10.27, p<0.90; df=5, χ^2=9.35, p<0.90; df=17, χ^2=11.36, p<0.90; df=5, χ^2=11.34, p<0.90). Therefore, comparisons of the mean proportion of particular size classes in females and males were done between particular habitat types and seasons.

The shell size differed between the sexes (ANOVA, p>0.05): females were larger than males (Tukey test, p<0.001). Most females belonged to classes III and IV while males were mainly represented by individuals of classes II and III (Fig. 8A and B). Only in the Narew River in the spring 29% of males were in class I. Class I constituted the smallest proportion (from 5 to 29%) among individuals of both sexes.

Size structure of female and male *V. contectus*

The size structure of males and females differed between the two types of oxbow lakes (ANOVA, p<0.001). As in the case of *V. viviparus*, females were larger than males (Tukey test, p<0.001). Females of size classes III and IV dominated over the whole phenological cycle (Fig. 9A). In the spring, summer and autumn most males belonged to classes II and III (Fig. 9B). The fewest males and females (from 7 to 18%) represented size class I.

Fecundity of *V. viviparus*

The percentage of gravid and non-gravid females and the mean number of embryos per female varied in a similar way (df=17, χ^2=9.37, p=0.81; df=5, χ^2=10.45, p=0.78 and df=17, χ^2=12.47, p=0.91; df=5, χ^2=8.49, p=0.89, respectively).

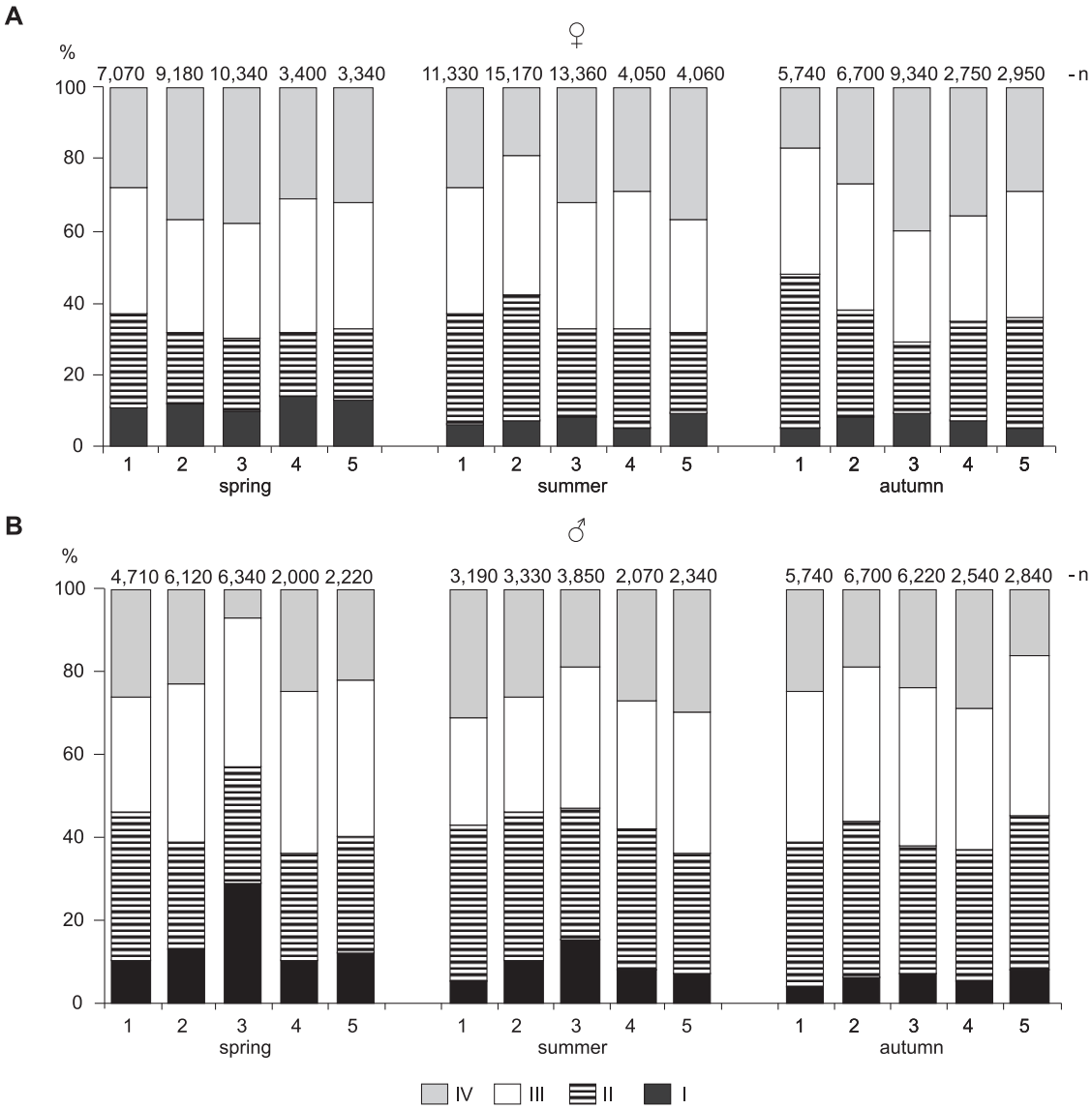

Fig. 8. Seasonal changes in the proportion of size classes (I–IV) among female (A) and male (B) *V. viviparus* in different habitats; 1–5 – see caption to Fig. 5; mean values of 1995–2008 (1–3), and 2003–2008 (4–5)

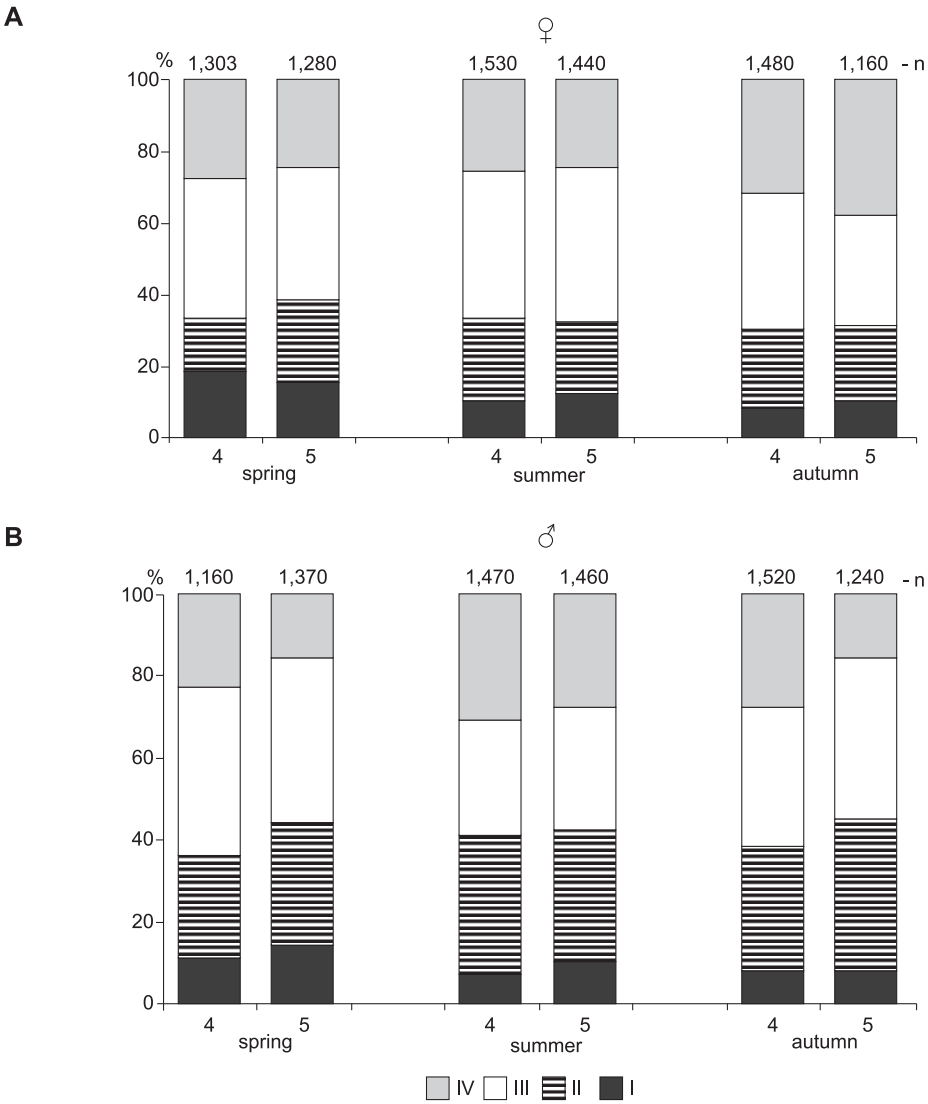

Fig. 9. Seasonal changes in the proportion of size classes (I–IV) among female (A) and male (B) *V. contectus* in flow (4) and isolated (5) oxbows; mean values of 2003–2008

Gravid females dominated (from over 50% to 90%) in all the habitats. In the summer their proportion was the highest and differed from that in the spring (G=8.20, p<0.005) and autumn (G=5.90, p<0.001) (Table 5). The percentage of gravid females was similar in the spring and autumn (G=5.90, p=0.31) with the exception of the flow oxbow lakes where the proportion of gravid females was the highest (90%) in the spring (Table 5).

The gravid females belonged to size classes II, III and IV (Fig. 10A). ANOVA showed an effect of season on the size structure of gravid females (p<0.001). Fe-

Table 5. Proportion [%] of gravid female *V. viviparus* in spring, summer and autumn in different habitats (numbers of individuals given in parentheses) (for 1–5 see Table 3)

Season	Habitats					G-test (df=3)
	1	2	3	4	5	
spring	60	70	62	90	64	spring/summer 8.20*
	(4,242)	(6,426)	(6,411)	(3,060)	(2,137)	
summer	78	80	75	75	73	summer/autumn 10.20*
	(8,837)	(12,136)	(10,020)	(3,037)	(2,963)	
autumn	55	60	58	65	55	autumn/spring 5.90,
	(3,157)	(4,020)	(5,417)	(1,787)	(1,285)	p=0.31 except for 4 11.90**

significance: *p<0.005, **p<0.001

males of classes II and III dominated in the spring. The proportion of class IV females increased in the summer and that of class III females – in the autumn, which was associated with the growth of snails and their transition into the next size class. The lack of snails from size class I resulted from the age at maturity which falls within class II, corresponding to females of the shell height between 8.1 and 12.0 mm.

Snails of size classes III and IV dominated among non-gravid females in the spring and summer. In the autumn their proportion decreased, together with the increase in the percentage of class II females (Tukey test, $p<0.001$) (Fig. 10B).

Multifactor GLM analysis showed that the habitat, season and shell height affected the fecundity to the greatest extent (Table 6). The shell width was the least significant factor in this respect.

The mean number of embryos per female varied among the habitats (Tukey test, $p<0.001$). The greatest number of embryos (mean 16.7) was noted in females from the flow oxbow lakes and those from the outlet sections of the rivers (mean 15.5), the fewest embryos were found in females from the isolated oxbow lakes (mean 7.9) and from the Zegrzyński Reservoir (mean 9.1) (Fig. 11).

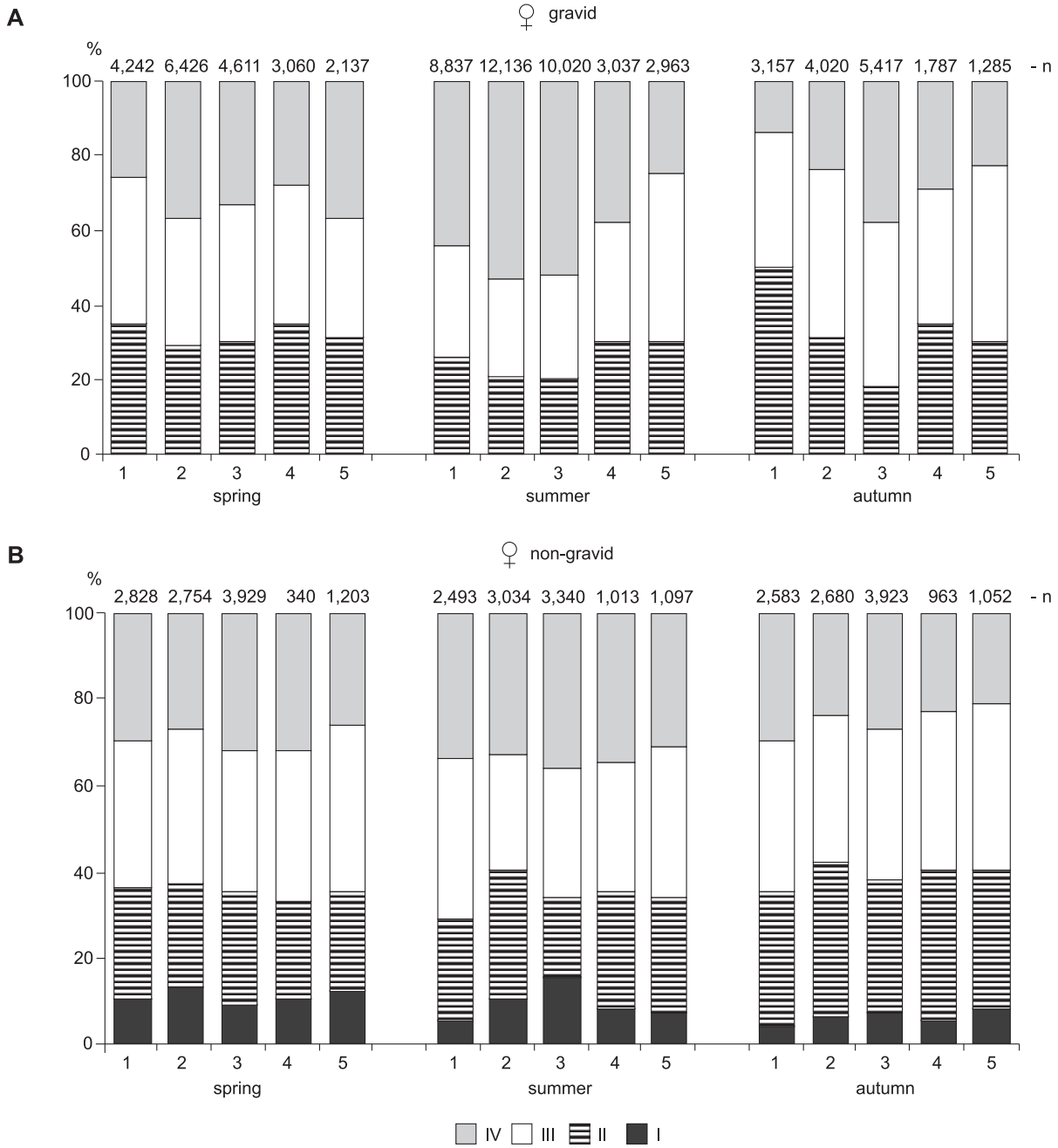

Fig. 10. Seasonal changes in the proportion of gravid (A) and non-gravid (B) female *V. viviparus* in size classes I–IV in different habitats; for 1–5 see caption to Fig. 5; mean values of 1995–2008 (1–3) and 2003–2008 (4–5)

Table 6. Multifactor GLM analysis of the effect of shell height, shell width, habitat, season and habitat × season on the mean number of embryos per female *V. viviparus*

Variable	Number of embryos per female		
	df	f	p
shell height	74935	57.48	0.001
shell width	74935	20.35	0.640
habitat	69518	247.52	0.001
season	86654	117.67	0.001
habitat × season	137870	47.32	0.001

The mean number of embryos per female varied seasonally (ANOVA, $p<0.001$). Statistically significant differences were noted in the mean number of embryos per female between the spring and summer (except the Zegrzyński Reservoir), spring and autumn and between the summer and autumn. There were no differences in the number of embryos between the spring and summer in females from the Zegrzyński Reservoir (Table 7, Fig. 11).

The number of embryos was the greatest in the spring and summer i. e. in the period of intensive reproduction; in the autumn the number was nearly two times lower (Newman-Keuls test, $p<0.001$). In the spring and summer the mean number of embryos per female was the highest in the flow oxbow lakes (17.7 and 22.7, respectively) and in the river outlets (15.4 and 20.8, respectively). The maximum number of embryos per female (70) was observed in the outlet sections of the rivers.

The highest values of the reproductive effort (IEI index) were noted in the flow lakes in the whole vegetation period (spring 1.68, summer 5.08, autumn 1.06) and the lowest – in the Zegrzyński Reservoir (spring 0.27, summer 0.38, autumn 0.21) (Table 8).

In most habitats the mean number of embryos per female differed significantly among the size classes (Table 9). The mean fecundity did not differ between the classes only in the autumn in the flow oxbow lakes and in the summer in the isolated oxbow lakes. In the dam reservoir, ecotone zones, the Narew River and the isolated oxbow lakes, the number of embryos increased with the females' size. The largest females (class IV) contained the highest number of embryos. The highest number of embryos per female (25) was noted in the ecotone habitats.

The females from the flow lakes showed the greatest fecundity when in size classes II and III. The mean number of embryos per female in class II (16) and class III (17) in the spring was higher than or similar to that in class IV females from the other habitats (Newman-Keuls test). The situation was similar in the summer when the fecundity of class II females (mean 16 embryos per female) was higher than that of the largest females in the dam reservoir (mean 13 embryos per female in class IV) or in the isolated oxbow lakes (mean 9 embryos per female) (Newman-Keuls test, $p<0.05$).

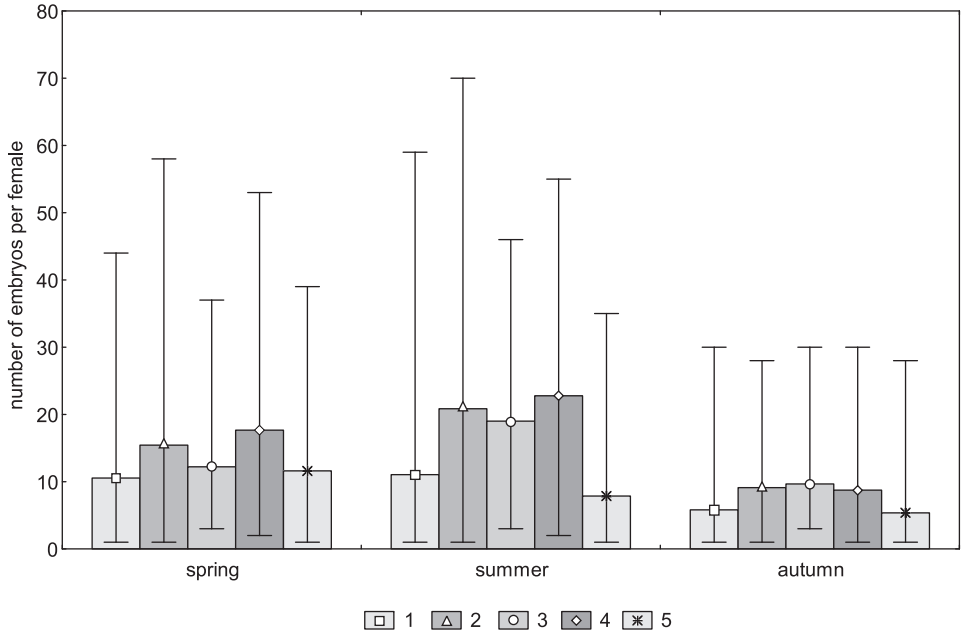

Fig. 11. Seasonal changes in the mean number of embryos per female *V. viviparus* in different habitats; for 1–5 see caption to Fig. 5; mean values of 1995–2008 (1–3) and 2003–2008 (4–5) with max – min ranges

Table 7. Significance of seasonal differences in the mean number of embryos per female *V. viviparus* in different habitats (for 1–5 see Table 3); ns – not significant

Habitat	spring – summer	spring – autumn	summer – autumn
1	ns	df=6049	df=6684
2	df=14137	df=14137	df=13804
3	df=17746	df=12952	df=12635
4	df=91935	df=2958	df=7718
5	df=4708	df=3874	df=1622

significance: p<0.001

Table. 8. Seasonal changes in reproductive effort (IEI) of female *V. viviparus* in different habitats (for 1–5 see Table 3)

Habitat	Season	N	Mean (±SD)	Newman-Keuls test
1	spring	4,242	0.27 (±0.18)	spring/summer*,
	summer	8,837	0.38 (±0.16)	spring/autumn, p=0.32,
	autumn	3,157	0.21 (±0.12)	summer/autumn*
2	spring	6,426	0.39 (±0.29)	spring/summer*,
	summer	12,136	1.45 (±0.87)	spring/autumn, p=023,
	autumn	4,020	0.37 (±0.15)	summer/autumn*
3	spring	6,411	0.36 (±0.27)	spring/summer*,
	summer	10,020	1.35 (±0.88)	spring/autumn, p=0.45,
	autumn	5,417	0.32 (±0.14)	summer/autumn*
4	spring	3,060	1.68 (±0.67)	spring/summer*,
	summer	3,037	5.08 (±2.18)	spring/autumn, p=022,
	autumn	1,787	1.06 (±0.24)	summer/autumn *
5	spring	2,137	0.31 (±0.16)	spring/summer*,
	summer	2,963	0.44 (±0.17)	spring/autumn, p=0.25,
	autumn	1,285	0.26 (±0.12)	summer/autumn *

significance: *p<0.05

Table 9. Comparison of the mean number of embryos/female *V. viviparus* in three size classes (II, III, IV) in different habitats (for 1–5 see Table 3); ns – not significant

Habitat	Size class	Spring			Summer			Autumn		
		N	Mean (±SD)	Newman-Keuls test	N	Mean (±SD)	Newman-Keuls test	N	Mean (±SD)	Newman-Keuls test
1	II	1,485	4.5(±1.91)	II/III*	2,298	7.0(±2.49)	II/III ns	1,578	3.7(±1.84)	II/III*
	III	1,654	12.4(±8.19)	II/IV*	2,651	10.1(±6.35)	II/IV*	1,136	7.1(±6.24)	II/IV*
	IV	1,103	10.4(±8.18)	III/IV, ns	3,888	13.0(±11.14)	III/IV*	442	10.81(±5.61)	III/IV*
2	II	1,863	8.0(±4.77)	II/III*	2,549	14.4(±7.63)	II/III ns	1,246	7.3(±3.85)	II/III*
	III	2,185	19.9(±11.45)	II/IV*	3,155	17.6(±8.49)	II/IV*	1,809	7.8(±7.48)	II/IV*
	IV	2,378	22.1(±11.45)	III/IV*	6,796	25.3(±15.70)	III/IV*	884	10.8(±5.61)	III/IV*
3	II	1,923	7.8(±3.78)	II/III*	2,004	13.7(±6.70)	II/III ns	975	6.9(±3.45)	II/III
	III	2,372	17.8(±10.23)	II/IV*	2,806	16.9(±7.40)	II/IV*	2,383	7.3(±4.53)	II/IV*
	IV	2,116	21.5(±10.89)	III/IV*	5,210	24.5(±14.50)	III/IV*	2,058	11.2(±5.23)	III/IV*
4	II	1,071	16.5(±9.23)	II/III	911	16.2(±8.73)	II/III*	625	8.3(±4.17)	II/III ns
	III	1,132	17.0(±8.27)	II/IV*	972	25.8(±10.77)	II/IV ns	643	9.6(±4.76)	II/IV ns
	IV	8,568	19.6(±11.63)	III/IV, ns	1,154	21.5(±12.02)	III/IV*	518	7.0(±5.22)	III/IV ns
5	II	662	4.4(±2.07)	II/III*	889	7.15(±2.50)	II/III ns	385	3.6(±1.79)	II/III*
	III	683	12.0(±8.75)	II/IV*	1,333	7.0(±4.53)	II/IV ns	604	6.4(±5.54)	II/IV*
	IV	790	13.0(±7.75)	III/IV ns	740	8.7(±4.63)	III/IV ns	321	5.1(±4.27)	III/IV*

significance: *p<0.05

The studies carried out in 1990–1994 in the Zegrzyński Reservoir and in the river outlets revealed a positive correlation between the mean number of embryos and the female's shell height, shell width, dry body weight and dry shell weight. The strongest correlation was found between the mean number of embryos and the dry body weight (Fig. 12) (JAKUBIK 2007).

The studies carried out since 1995 showed a similar correlation, except the flow oxbow lakes. The mean number of embryos increased with the shell height and width. The strongest correlations were found in snails from the Narew River ($r=0.50$, $n=1{,}213$, $p<0.005$ for shell height, $r=0.49$, $n=1{,}213$, $p<0.005$ for shell width and $r=0.65$, $n=1{,}213$, $p<0.005$ for dry body weight). The correlation between the number of embryos and these parameters was the weakest for snails from the isolated oxbow lakes ($r=0.27$, $n=354$, $p<0.001$ for shell height, $r=0.24$, $n=354$, $p<0.001$ for shell width and $r=0.35$, $n=354$, $p<0.001$ for dry body weight). The respective correlation coefficients for snails from the flow oxbow lakes were, however, negative indicating a decrease in the mean number of embryos with increasing shell size ($r=-0.44$, $n=438$, $p<0.001$ for shell height, $r=-0.34$, $n=438$, $p<0.001$ for shell width) and body weight ($r=-0.75$, $n=438$, $p<0.001$) (Fig. 13). This observation agrees with the earlier analyses of the mean number of embryos per female in particular size classes. They showed a high fecundity of class II females which was similar to that in females from the other habitats. It seems that snails in the flow oxbow lakes reproduced earlier. At that age viviparids attained class II size and they remained in that class till the end of field observations (November of the first year). In the second year of observations (May) the shell size exceeded that of class III.

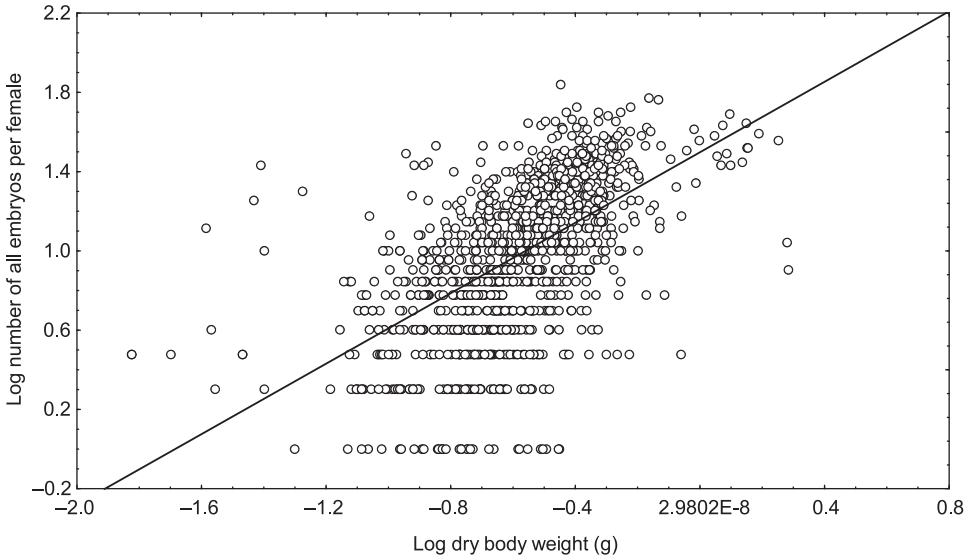

Fig. 12. Number of embryos per female *V. viviparus* against dry body mass [g] in the Zegrzyński Reservoir, mean values of 1990–1994 (after JAKUBIK 2007)

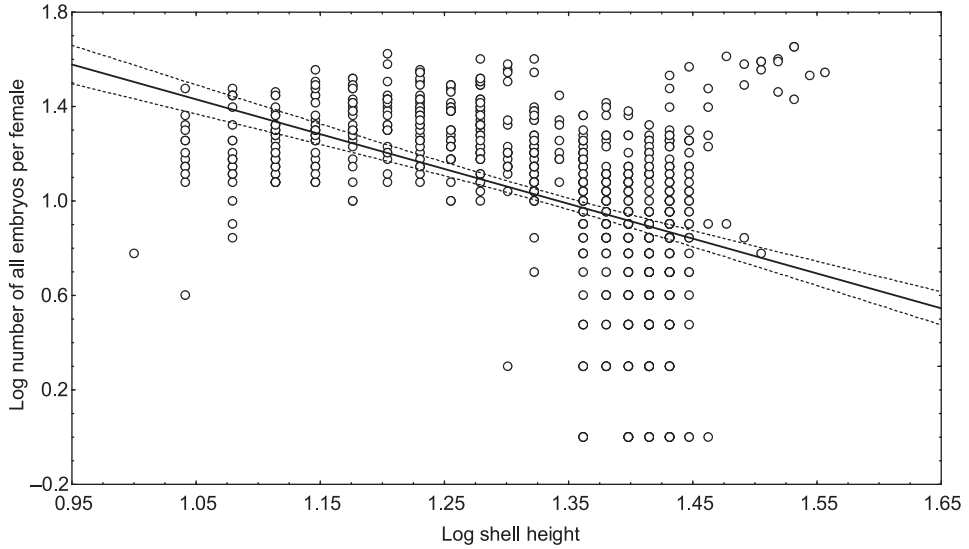

Fig. 13. Number of embryos per female *V. viviparus* against shell height [mm] in flow oxbows (4); mean values of 2003–2008

Fecundity of *V. contectus*

Gravid females dominated (from 60% to 90%) among females in both flow and isolated oxbow lakes. Their proportion, as in *V. viviparus,* varied seasonally, being high in the summer and statistically different from that in the spring and autumn (Table 10). In the studied habitats gravid females belonged to size classes II, III and IV (Fig. 14A). ANOVA showed the effect of season on the size structure of gravid females ($p<0.001$). Snails of classes II and III dominated in the spring and summer ($p<0.001$). The proportion of individuals from class III increased in the summer and that of the largest snails – in the autumn, as a result of growth.

Non-gravid females represented all size classes (Fig. 14B). The mean number of embryos per female significantly differed between the types of oxbow lakes

Table 10. Proportion [%] of gravid and non-gravid female *V. contectus* in spring, summer and autumn in flow oxbows (4), and isolated oxbow (5) (numbers of individuals given in parentheses)

Season	Habitats		G-test (df=3)
	4	5	
spring	87	68	spring/
	(1,133)	(841)	summer 5.20*
summer	90	77	summer/
	(1,377)	(1,108)	autumn 8.20*
autumn	67	58	autumn/
	(991)	(672)	spring 4.90 *

significance: *p<0.005

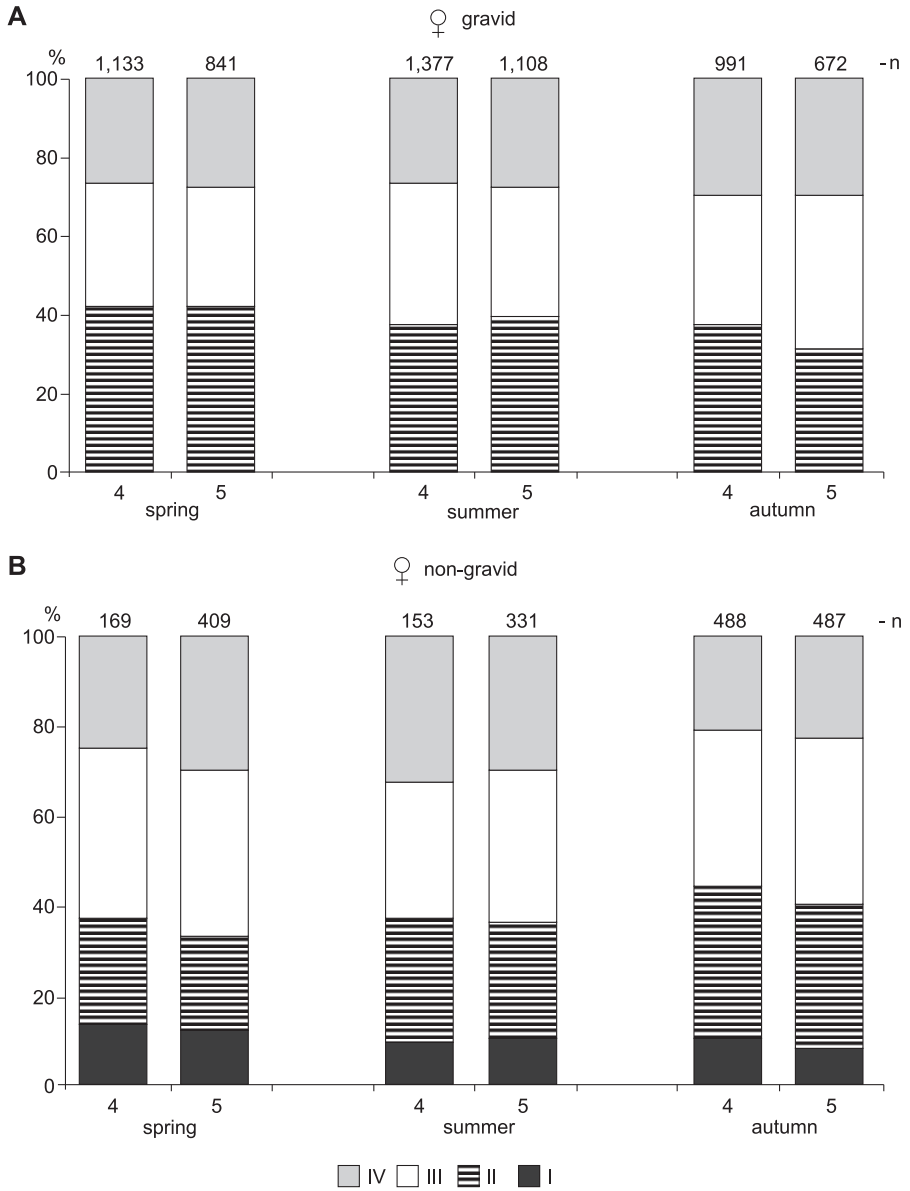

Fig. 14. Seasonal changes in the proportion of gravid (A) and non-gravid (B) female *V. contectus* in age classes I–IV in flow (4) and isolated (5) oxbows; mean values of 2003–2008

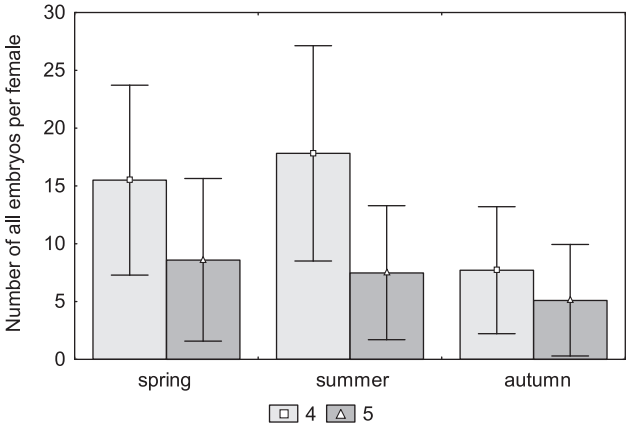

Fig. 15. Seasonal changes in the mean number of embryos per female *V. contectus* in flow (4) and isolated (5) oxbows; mean values of 2003–2008 with max – min ranges

Table 11. Multifactor GLM analysis of the effect of shell height, shell width, habitat, season and habitat × season on the mean number of embryos per female *V. contectus*

Variable	Number of embryos per female		
	df	f	p
shell height	6122	57.34	0.001
shell width	6122	39.25	0.541
habitat	7322	98.12	0.001
season	7322	67.12	0.001
habitat × season	15240	49.23	0.001

Table 12. Significance of seasonal differences in the mean number of embryos per female *V. contectus* in flow oxbows (4), and isolated oxbow (5)

Habitat	spring – summer	spring – autumn	summer – autumn
4	df=513, p<0.001	df=462, p<0.001	Df=519, p<0.001
5	df=510, p<0.001	df=576, p=0.07	Df=636, p<0.001

(Tukey test, p<0.001). In the flow lakes the mean number of embryos per female was 13.9 and in the isolated oxbows it was half that and amounted to 6.8 (Fig. 15).

Based on multifactor analyses the parameters affecting the fecundity were shell height and width, habitat and season (Table 11); they were the most important for the fecundity. The least significant effect was exerted by the shell width.

ANOVA showed the effect of season on the mean number of embryos per female (Newman-Keuls test, p<0.001). Significant differences in this parameter were found between the spring and summer (except the isolated lakes), between the spring and autumn and between the summer and autumn (Table 12, Fig. 15). In both types of oxbow lakes the greatest fecundity was observed in the summer (17.8 embryos per female in the flow lakes and 7.5 in the isolated lakes) and in the spring (15.5 and 8.6 embryos per female, respectively). The maximum numbers of embryos per female (45 in the flow lakes and 35 in the isolated lakes) were also noted in these seasons.

The reproductive effort (IEI) of *V. contectus*, like its fecundity, was higher in the flow lakes (Tukey test, p<0.001). ANOVA showed the effect of season (p<0.001) on the reproductive effort (except the differences between spring and autumn in the isolated lakes) (Table 13).

The fecundity of class II females in the flow lakes was higher than or similar to that of class IV females in the isolated lakes (Table 14) (Newman-Keuls test, p<0.001). In the isolated lakes the number of embryos per female depended on the body and shell parameters which was shown by the analysis of correlation coefficients. The mean number of embryos increased with these parameters (r=0.47, n=1,064, p<0.005 for shell height, r=0.35, n=1,064, p<0.005 for shell width and r=0.45, n=1,064, p<0.005 for dry body weight).

In the flow oxbow lakes the correlation coefficients were negative indicating, as they did in the case of *V. viviparus*, the increase in the mean number of embryos with decreasing shell size (r=–0.45, n=1,314, p<0.005 for shell height and r=–0.33, n=1,314, p<0.005 for shell width) and dry body weight (r=–0.68, n=1,314, p<0.005) (Fig. 16).

Table 13. Seasonal changes in reproductive effort (IEI) of female *V. contectus* in flow (4) and isolated (5) oxbows

Habitat	Season	N	Mean (±SD)	Newman-Keuls test
4	spring	1,133	0.79 (±0.36)	spring/summer*
	summer	1,377	1.74 (±0.68)	spring/autumn*,
	autumn	991	0.53 (±0.24)	summer/autumn *
5	spring	841	0.24 (±0.16)	spring/summer*
	summer	1,108	0.41 (±0.15)	spring/autumn, p=0.67
	autumn	672	0.22 (±0.10)	summer/autumn *

significance: *p<0.05

Table 14. Comparison of the mean number of embryos/female *V. contectus* in three size classes (II, III, IV) in flow (4) and isolated (5) oxbows

Habitat	Size class	spring			summer			autumn		
		N	Mean (± SD)	Newman-Keuls test	N	Mean (± SD)	Newman-Keuls test	N	Mean (± SD)	Newman-Keuls Test
4	II	1,020	11.7 (± 2.81)	II/III* II/IV* III/IV*	1,207	13.7 (± 2.40)	II/III* II/IV* III/IV	860	5.2 (± 1.24)	II/III* II/IV* III/IV*
	III	1,115	13.7 (± 7.19)		1,467	16.6 (± 4.35)		950	9.7 (± 1.21)	
	IV	1,450	15.3 (± 3.11)		1,358	15.6 (± 7.14)		854	7.0 (± 2.11)	
5	II	897	5.5 (± 4.23)	II/III* II/IV* III/IV*	879	6.9 (± 3.43)	II/III* II/IV* III/IV*	675	3.8 (± 1.28)	II/III* II/IV* III/IV*
	III	1,016	8.4 (± 2.21)		990	9.8 (± 3.77)		798	5.4 (± 1.76)	
	IV	1,020	11.9 (± 8.63)		1,023	13.8 (± 8.03)		970	8.7 (± 1.42)	

significance: *p<0.05

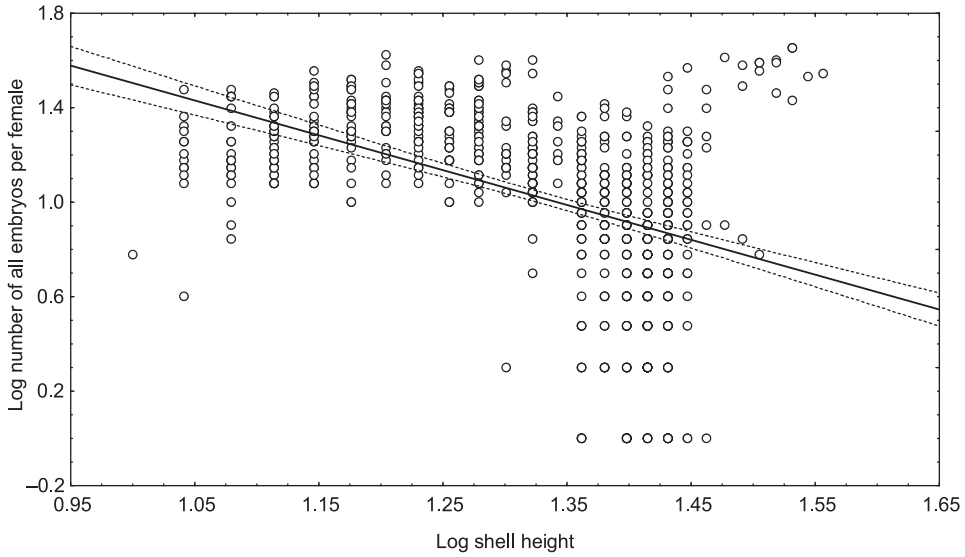

Fig. 16. Number of embryos per female *V. contectus* against shell height [mm] in flow oxbows (4); mean values of 2003–2008

EMBRYONIC GROWTH PATTERN

Embryonic growth pattern in *V. viviparus*

The studies on embryonic growth in 1990–1994 in the Zegrzyński Reservoir and in the ecotone habitats (outlet sections of the Bug, Narew and Rządza rivers) revealed dominance of the youngest and the oldest embryos in females of all size classes (Fig. 17) (JAKUBIK 2007). A similar proportion of embryos of different stages was also noted in 1995–2008. The youngest (from 30% to 65% of all embryos) and the oldest (20–49%) embryonic stages dominated in females from the studied reservoirs and river sections. Medium-size embryos constituted a smaller proportion (from 10% to 30%) (Fig. 18).

The mean number of embryos in particular growth stages varied among the seasons which was shown by variance analysis (Table 15). The high percentage of the youngest embryos during the whole vegetation season indicates that the reproduction period lasted from spring till autumn.

The considerable proportion of the oldest embryos in the spring could be an effect of embryo

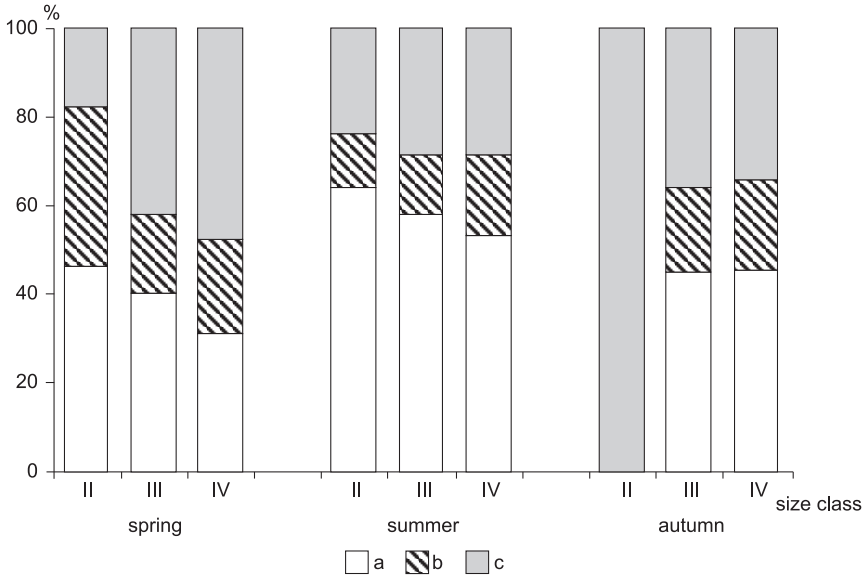

Fig. 17. Seasonal changes in the proportion of embryos at different development stages (a – youngest, b – medium, c – oldest) in *V. viviparus* in age classes I–IV in different habitats; mean values for all sites given for 1990–1994 (after JAKUBIK 2007)

retention during the winter. The same situation in the summer may result from development of medium-advanced embryos. In the autumn the proportion changed to the advantage of the oldest embryos which was a natural consequence of the growth of embryos and their retention till the next vegetation season. The high fecundity in the spring is the outcome of this phenomenon.

The studies carried out in 1990–1994 showed that in *V. viviparus* the mean number of the oldest embryos (snails with fully developed shells) increased with the female's shell height and width and with dry shell weight (JAKUBIK 2007). The mean number of the youngest embryos (oval, transparent egg capsules) increased with the female's dry body weight (Fig. 19 A and B).

Similar relationships were noted for the populations of *V. viviparus* in 1995–2008. In the reservoir, the outlet zones and the river, the number of the oldest embryos (with developed shells) increased with the female's shell height ($r=0.49$, $n=1,629$; $r=50$, $n=1,816$; $r=45$, $n=1,458$, $p<0.001$, respectively), shell width ($r=0.41$, $n=1,629$; $r=0.47$, $n=1,816$; $r=0.40$, $n=1,458$, $p<0.001$, respectively) and dry shell weight ($r=0.45$, $n=1,629$; $r=0.49$, $n=1,816$; $r=0.42$, $n=1,458$, $p<0.001$, respectively).

Table 15. Significance of seasonal differences in the mean number of embryos per female *V. viviparus* in different habitats (for 1–5 see Table 3); ns – not significant

Habitats	Mean number of embryos per female	spring – summer	spring – autumn	summer – autumn
1	youngest	df=9,875	df=9,470	df=9,989
	medium	df=4,567	df=4,670	ns
	oldest	ns	ns	ns
2	youngest	df=10,114	df=11,780	df=10,809
	medium	df=5,678	ns	df=5,089
	oldest	df=8,780	df=8,578	df=8,908
3	youngest	df=12,340	df=12,109	df=11,809
	medium	ns	ns	ns
	oldest	df=9,800	df=9,704	df=9,456
4	youngest	ns	df=8,679	df=8,568
	medium	ns	df=4,560	ns
	oldest	ns	df=7,578	df=7,657
5	youngest	ns	df=10,235	df=10,125
	medium	df=2,047	ns	df=2,135
	oldest	df=8,670	df=8,689	ns

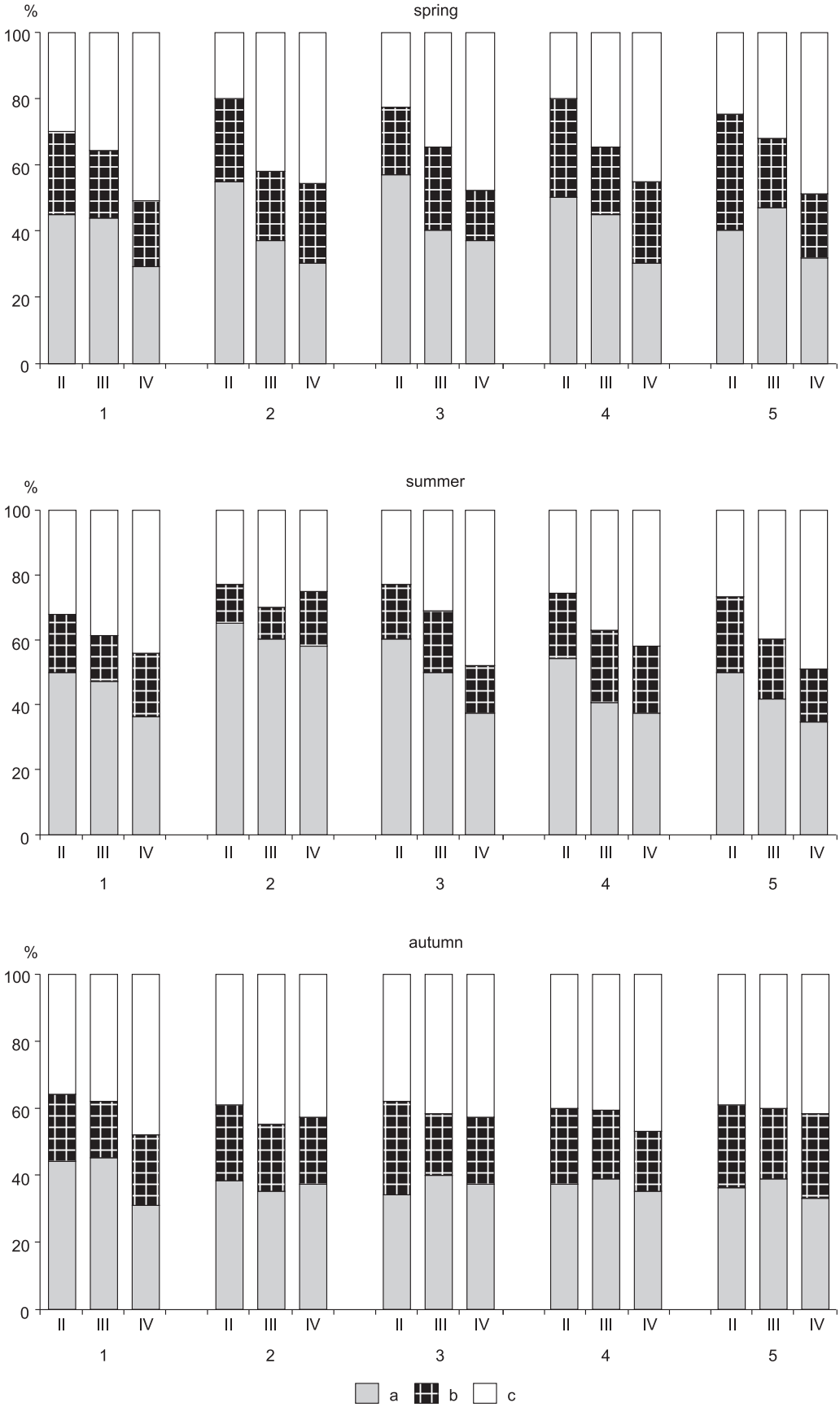

Fig. 18. Seasonal changes in the proportion of embryos at different development stages (a – youngest, b – medium, c – oldest) in *V. viviparus* in age classes I–IV in different habitats; for 1–5 see caption to Fig. 5; mean values of 1995–2008 (1–3) and 2003–2008 (4–5)

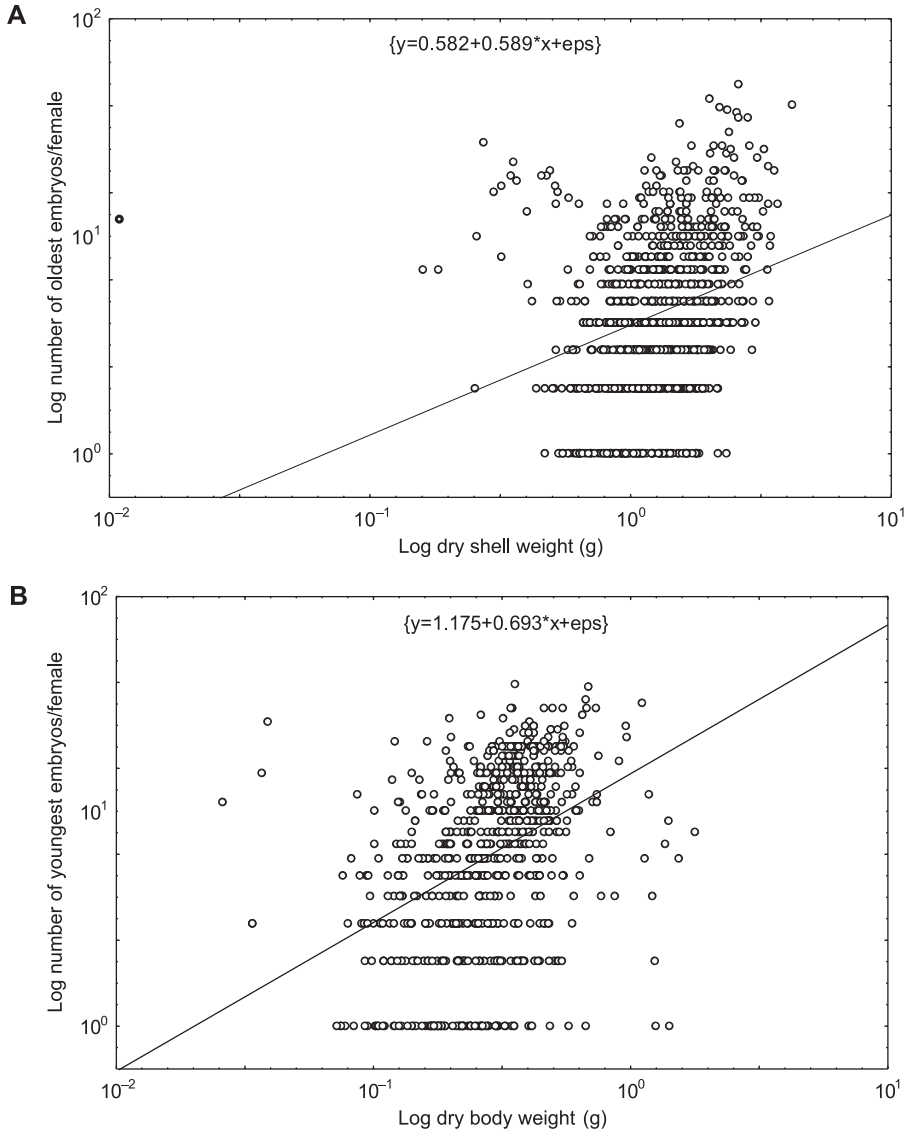

Fig. 19. *V. viviparus* – number of oldest embryos against female shell height (A); number of youngest embryos against female dry body mass (B); mean values for all sites given for 1990–1994 (after JAKUBIK 2007)

The number of medium-sized embryos did not correlate with the female's shell and body parameters. These embryos were on the transition between the youngest and the oldest, and their proportion in the brood chamber was the smallest, compared to the other embryonic stages.

In snails from the isolated oxbow lakes the number of youngest and oldest embryos was most closely correlated with the female's shell height (r=0.38, n=1,131, p<0.05 and r=0.22, n=964, p<0.05, respectively). The correlation was most significant and positive for the youngest embryos. The female's dry body weight did not affect the number of embryos in particular growth stages. The number of youngest embryos in snails from the flow oxbow lakes showed a negative correlation with the female's shell height (r=–0.56, n=1,067, p<0.05) (Fig. 20). The female's dry body weight did not affect the number of the youngest and medium embryos. A significant correlation was, however, found between the number of the oldest embryos and the female's dry body weight (r=0.67, n=846, p<0.05).

Embryonic growth pattern in *V. contectus*

The embryonic growth pattern in *V. contectus* – with the dominance of the youngest and oldest stages – was similar to that in *V. viviparus*. The season clearly affected the percentage of particular embryonic stages. The youngest embryos dominated in the spring and summer, and in the autumn the oldest embryos constituted a greater proportion. In the isolated oxbow lakes the number of oldest embryos increased with the female's shell height and width, and the female's body weight influenced the number of the youngest embryos. The number of medium-sized embryos was not correlated with the shell and body parameters. As in *V. viviparus*, the number of youngest em-

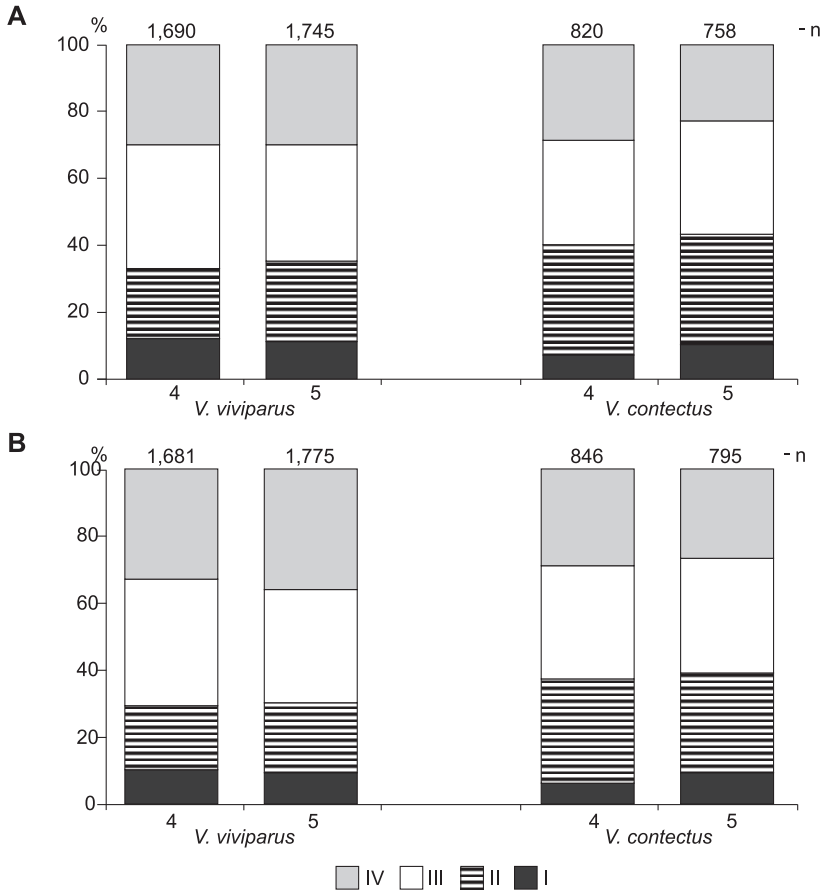

Fig. 20. Number of youngest embryos against female shell height in *V. viviparus* from flow oxbows; means of 2003–2008

bryos was negatively correlated with the female's shell height ($r=-0.73$, $n=897$, $p<0.05$).

EXTENSITY OF INFECTION OF *V. VIVIPARUS* AND *V. CONTECTUS* BY TREMATODE LARVAE

Viviparids infected by trematode larvae dominated in both types of oxbow lakes. The extensity of infection was high and reached 95% in the flow lakes and 90% in the isolated lakes for both viviparid species. The snails were infected by three trematode species: *Amblosoma exile*, *Neocanthoparyphium echinatoides* and *Leucochloridiomorpha lutea*. *A. exile* (92% in *V. viviparus* and 83% in *V. contectus*) was the most frequent trematode in the flow lakes. In the isolated lakes most viviparids were infected by *N. echinatoides* (95% in *V. viviparus* and 90% in *V. contectus*).

DISCUSSION

The long-term studies on the viviparid life strategies in various aquatic habitats of Poland have made it possible to distinguish two groups of life history traits: 1. constant and independent of the habitat type, and 2. varying under the effect of different ecological conditions. The first guarantee maintaining a relatively stable population density, the second offer a possibility of adjustment to local conditions.

Maintaining population density in Viviparidae, as in all dioecious organisms, depends on the sex ratio, age structure and on the proportion of gravid females in the population. The density and biomass of the studied snails varied only slightly between consecutive years of the studies. The seasonal dynamics of density and biomass was similar in all the habitats. In the summer the viviparids formed aggregations in the near-shore zones; markedly smaller densities were observed in the spring and autumn. In the autumn the snails migrated deep into the reservoir and rivers to overwinter in the bottom sediments.

In the spring the snails started to move toward the shore where they formed aggregations in the same places as in the preceding year. The pattern was repeated every year and indicated a high stability of the studied populations. The same patterns of viviparid occurrence were reported by e.g. ZHADIN (1928, 1952), MIROSHNICHENKO (1958), STAŃCZYKOWSKA (1959, 1960a, b), STAŃCZYKOWSKA et al. (1971), SA-

MOCHWALENKO & STAŃCZYKOWSKA (1972), JOKINEN (1982, 1992), LEVINA (1992), ZHOKHOV (1993), ZETTLER (1996), and JAKUBIK (2003) in rivers, oxbow lakes, lakes and dam reservoirs. Migrations of *V. contectus* deep into water bodies were described by ELEUTHERIADIS & LAZARIDOU-DIMITRIADOU (1995), those of *V. georgianus* – by LEE et al. (2002), and those of *Cipangopaludina japonica* – by TAKI (1981). Similar migrations deep into lakes or rivers were also observed in other species of Caenogastropoda, e.g. in *Theodoxus fluviatilis* (SKOOG 1971), *Amnicola limosa* (HORST & COSTA 1975), *Bithynia tentaculata* (VINCENT et al. 1981) and *Bithynia graeca* (ELEUTHERIADIS & LAZARIDOU-DIMITRIADOU 1995).

The characteristic pattern of occurrence of Viviparidae makes their populations large enough to dominate the benthic fauna of rivers and lake littoral (STAŃCZYKOWSKA 1960a, b, JAKUBIK & STAŃCZYKOWSKA 1996, JURKIEWICZ-KARNKOWSKA 1998, LEWANDOWSKI 2004). Such phenomenon was long observed in the Zegrzyński Reservoir (JURKIEWICZ-KARNKOWSKA 1986, DUSOGE 1989, LEWANDOWSKI et al. 1989, STAŃCZYKOWSKA et al. 1990, DUSOGE et al. 1999, JAKUBIK 2003).

Among the studied populations, the highest density of *V. viviparus* was recorded in the outlet sections of the Bug, Narew and Rządza rivers and in the Narew itself (mean 500 ind. m^{-2}); it was smaller in the Zegrzyński Reservoir (265 ind. m^{-2}) and the smallest in the flow and isolated oxbow lakes (mean 150 ind. m^{-2} and 120 ind. m^{-2}, respectively). The biomass followed the same pattern. The population density in particular habitats was similar from year to year. The habitat selection by snails was probably associated with seeking appropriate environmental conditions – water aeration and hard bottom: sand or gravel with mud admixture, or rarely mud and sediments enriched with organic matter (ZHADIN 1940, STAŃCZYKOWSKA et al. 1971, 1972, PLIŃSKI et al. 1978, JOKINEN 1985, JAKUBIK 2003). ZHADIN (1940) presented the ecological spectrum of *V. viviparus*, considering the range of habitat conditions. According to him, *V. viviparus* prefers habitats of medium values of such factors as e.g. water transparency, temperature, pH, and calcium and organic matter content. In this study such conditions were met in the case of pH, oxygen and calcium concentration in all the sites with abundant viviparid populations. The high density observed in the outlet section of the Narew River could result from the ecotone character of this habitat. The studied habitats differed mainly in the concentration of organic matter, phosphorus and nitrogen in the water and bottom sediments. Similar or even higher density and biomass of viviparids were found by STAŃCZYKOWSKA (1960b) in the Konfederatka Shoal of the Vistula. The maximum snail densities reached 2,700 ind. m^{-2} in the summer, in the zone of occurrence of young individuals. The water body is comparable to the oxbow lakes of the Bug River. Its characteristic feature is a wide variability associated with annual water flow fluctuations (lotic and lentic phase), depending on the water level in the Vistula. Therefore, the water body is alternately stagnant or flowing. The oxbow lakes of the Bug River are only joined to the river but water does not flow through them.

The autumn decrease in the vivipard density in all the aggregations was largely associated with the autumn migration of the snails deep into the lake or river. Earlier studies in the Konfederatka Shoal (STAŃCZYKOWSKA 1960b), in the Zegrzyński Reservoir and in the river outlets (JAKUBIK 2003) associated this phenomenon also with dying out of male *V. viviparus* during their winter migration deep into the water bodies. The conclusion was supported by a distinct change of the sex ratio. The female:male ratio was 1:1 in the autumn but 2:1 next spring. Greater differences in the sex ratio were observed in 1995–2008. The sex ratios differed, however, between the summer and other seasons, when the number of females was four times that of males. This may have resulted from the fact that reproduction was the most intensive in late spring and early summer, and the probability of finding females in the habitat was much higher than in other seasons. The female:male ratio reported by BROWNE & RUSSELL-HUNTER (1978) for American populations of *V. georgianus* in several lakes near New York in the summer was 4:1.

In general, the equal female:male ratio in *V. contectus* and the predominance of females in *V. viviparus* agree with the literature data (PIECHOCKI 1979, FALNIOWSKI 1989a, ELEUTHERIADIS & LAZARIDOU-DIMITRIADOU 1995, RIBI 1999).

The size structure of Viviparidae was similar in all the studied habitats. Individuals of size classes II, III and IV prevailed there. Their proportion varied seasonally. Individuals of class II dominated in the spring and grew in the summer and autumn, to attain size of classes III and IV. Considering the substantial proportion of class II snails in the spring samples, it may be assumed that shell growth starts in early spring (already in March) or that it does not stop in late autumn. Observations in the Swedish Lake Mälaren (HUBENDICK 1948) demonstrated that 33% of the snails' growth took place before their first winter.

In the studied populations females were slightly larger than males (by one size class); the difference is associated with ovoviviparity and specific embryonic growth of these snails. Viviparidae are iteroparous snails living in seasonal habitats. Being invertebrates, they display a reproductive strategy which is partly similar to that of higher vertebrates. This pertains to the differences in body size. The female's body size ought to be adapted to production of the optimum number of offspring, while the male reproductive success relies on the number of fertilised females rather

than on their quality (e.g. WILLIAMS 1975, GILBERT & WILLIAMSON 1983).

Field studies in the oxbow lakes of the Bug River and laboratory studies (JAKUBIK & LEWANDOWSKI 2007) showed that the shell dimensions in viviparid neonates varied very little (shell height=4.0 mm and shell width=4.5 mm). This means that the initial body size did not affect the snail size in later life. In the first year of life, the growth was fast and the increments were equal for both sexes. In the second year females grew faster than males, and this regularity was maintained also in the third and fourth year of life.

The obtained results indicate that the large proportion of gravid females (mainly of size classes III and IV) ensures the high biomas and density of the studied populations. This is an effective life strategy in various habitats. The relatively stable and/or high population density is also guaranteed by survival till maturity. Most freshwater molluscs become mature before completing their shell growth (BUCKLEY 1986, STAŃCZYKOWSKA & LEWANDOWSKI 1995, LEWANDOWSKI 1996, 2001, LEWANDOWSKI et al. 1997, ELEUTHERIADIS & LAZARIDOU-DIMITRIADOU 2001, CZARNOŁĘSKI et al. 2003, 2005); the same pertains to some terrestrial gastropods (WIKTOR 2004).

In the studied populations the percentage of the youngest snails (size class I) was small in both sexes. Two explanations of this situation, both pertaining to the further fates of such individuals, can be proposed. The first assumes that young snails spend the first period of their life outside the aggregations of adults which may increase their mortality due to potential attack of predators (DE BERNARDI et al. 1976a, b, BROWNE 1978, BUCKLEY 1986, KHMELEVA et al. 1995). The second assumes that if snails migrate below e.g. 6 m depth, as was the case in populations of *V. ater* in Lake Zürich, Switzerland, then the mortality due to predator's attack will be small (KELLER & RIBI 1993). Such snails may grow to attain the size of classes II and III and only then return to the shallow littoral zone to attain high densities (KELLER & RIBI 1993). None of these hypotheses was confirmed by the results presented here. At a high juvenile mortality the studied populations would not achieve such high densities. Moreover, the maximum depth of the studied habitats was enough to provide refuge from potential predators. It seems that the very small percentage of the youngest snails is a result of their rapid growth which makes them move to the next size class already in the first month of life. This explanation was experimentally confirmed (JAKUBIK & LEWANDOWSKI 2007).

The great abundance of viviparids recorded in some sites may sometimes result from the accidental character of single observations, for example a single sampling made by LEWANDOWSKI et al. (1989) in the Zegrzyński Reservoir in June 1983. The dominance of the youngest individuals (90%) was noted in shallow places to the depth of 2 m. In deeper places they comprised nearly 50% of all *V. viviparus*. Actual trends of spatial and temporal changes reveal themselves only during frequent and long-lasting observations.

The studies on the size structure of Viviparidae in various habitats indicate that their aggregations are not composed of snails of one size class, though they contain mainly mature individuals. The dominance of adults is the effect of the fact that Viviparidae are perennials.

From among various models of life cycles of freshwater snails proposed by CALOW (1978) the viviparids correspond to model G, with the reproductive period extending to include spring and summer.

The greatest numbers of embryos in the females' uteri were observed in the summer; they were slightly smaller in the spring and markedly lower in the autumn. The differences in the number of embryos per female between the autumn and spring suggest that the reproduction period – giving birth to the "winter" embryos – starts in early spring. The higher percentage of gravid females in the spring compared to autumn, together with the greater proportion of females in the population, indicate a smaller winter mortality of females, compared to males. The ultimate effect is associated with the retention of embryos often observed in female viviparids in winter (ELEUTHERIADIS & LAZARIDOU-DIMITRIADOU 1995). Such phenomenon was also reported for other species of Viviparidae, e.g. for *V. georgianus* (BUCKLEY 1986) or for *V. ater* (DE BERNARDI et al. 1976b).

The fecundity differed among the five studied habitat types. In the case of *V. viviparus* the greatest numbers of embryos were found in females from the flow oxbow lakes (mean 16.7) and river outlets (mean 15.5). The fewest embryos were recorded in females from the isolated oxbows (mean 7.9) and from the Zegrzyński Reservoir (mean 9.1 embryos per female). The fecundity of *V. contectus* was of the same order and the mean was 13.9 embryos in the flow lakes and 6.8 in the isolated ones.

The literature data on the fecundity of *V. viviparus* and *V. contectus* show discrepancies. FRÖMMING (1956) reported 10 embryos per female *V. viviparus*, PIECHOCKI (1979) once noted over 80 embryos per female (mean 20) and FALNIOWSKI (1989a) – from 24 to 73 embryos per female (mean 50). SAMOCHWALENKO & STAŃCZYKOWSKA (1972) recorded from 15 to 30 embryos per female *V. contectus* and FALNIOWSKI (1989a) – from 1 to 67, most often 20–30 embryos per female. Data on the fecundity in other representatives of Viviparidae are equally diverse. RIBI & GEBHARDT (1986) found a mean of 15 to 20 embryos per female *V. ater* from Lake Zürich and Lago Maggiore, JOKINEN (1992) and VAIL (1978) – from 4 to 81 embryos per female (mean 11) for an American population of *V. georgianus*. Much higher maximum numbers of embryos per female (102 – 162) were given by JOKINEN

(1982) for *V. malleatus*. The mean numbers of embryos of *V. viviparus* and *V. contectus* presented in this paper were thus close to the average numbers reported in the literature for other species of Viviparidae, but were much smaller than the number of eggs produced by some oviparous snails. For example, the number of eggs per cocoon in oviparous *Lymnaea stagnalis* is 120 and the snail lays 60–150 cocoons a year (ZHADIN 1952). The difference in fecundity between oviparous and ovoviviparous snails is associated with the necessity to retain embryos in the reproductive system in the latter species. The retention of embryos and the extended time during which juveniles with fully developed shells are born provide a kind of protection from environmental factors. Therefore, the smaller number of embryos allows ovoviviparous snails to maintain high densities. Despite various ways of protecting egg capsules in oviparous species, they need to produce much more numerous eggs to maintain relatively high population density.

The differences in the fecundity of viviparids between the studied habitats were, among other factors, affected by habitat conditions, mainly by organic matter, phosphorus and nitrogen content in the bottom sediments (Table 2). Most of these substances were found abundantly in the river outlet sections and in the isolated Lake Białe which means that the food conditions were favourable there and resulted in greater fecundity.

Viviparidae acquire most of their food with the radula, but they can facultatively become filter feeders (FRETTER & GRAHAM 1978). The viviparid diet consists mainly of algae scraped with the radula, higher aquatic plants and detritus (FRÖMMING 1956, STAŃCZYKOWSKA et al. 1972, PIECHOCKI 1979, JAKUBIK 2009a). Besides, the snails filter small planktonic organisms like algae (Flagellata, Protococcales, Volvocales, Bacillariophyceae), bacteria, rotifers and detritus from the water (HÖCKELMANN & PUSCH 2000). ZHADIN (1928) found small sand grains, carapaces of Cladocera, sponge spiculae and nematodes in the intestines of the snails. According to FRÖMMING (1956), food of animal origin is necessary for normal growth of viviparids.

The studies on the feeding habits of *V. viviparus* showed that the available food resources constituted the main factor affecting food selection (JAKUBIK 2009a). The habitats analysed in this study differed considerably in this respect. The river outlet sections, rich in suspension and nutrients carried by the rivers, are favourable habitats for filter-feeders like Viviparidae; this was confirmed by the high fecundity of *V. viviparus*. In the isolated oxbow lake – Lake Białe – with its high content of organic matter of terrestrial origin, conditions for filter-feeders are less favourable. The sedimentation rate in Lake Białe is the greatest in the autumn while the reproduction of *V. viviparus* is the most intensive in the spring and summer.

The Zegrzyński Reservoir is a complex and variable water body which acts as a settling tank for the seston delivered by its tributaries (JURKIEWICZ-KARNKOWSKA 2004). In the stagnant part of the reservoir, the seston concentration may vary considerably over short periods as a result of increased sedimentation and decreased current velocity (KAJAK 1990). Such variable habitat conditions may decrease availability or physiological assimilability of food which may have resulted in a smaller fecundity of viviparids. On the other hand, the unidirectional water flow in rivers makes nutrients and food particles less available to potential consumers. They are lost if not consumed at once (REYNOLDS et al. 1991).

In the spring, the flow oxbow lakes are flooded by the waters of the Bug River which later returns a part of the delivered organic matter back to the river channel. Oxbow lakes, usually small and shallow, are functionally comparable with lake littoral which is the most diverse lake zone. Organic matter settling in these lakes is of autochthonous origin or is delivered with the surface runoff (e.g. terrestrial plant remains). Productivity of such reservoirs is affected by their connection with the river which brings organic and mineral matter and thus offers favourable food conditions for snails and other invertebrates.

The IEI indices calculated in this study showed different reproductive effort of Viviparidae in the analysed habitats. The index for females from the flow lakes was markedly higher than that for snails from other habitats. This indicates a negative correlation between the reproductive effort and the body size. According to the literature data, the reproductive abilities of most freshwater snails are a function of adult body size (e.g. DILLON 2000, NORTON & BRONSON 2006). This relationship was highly significant in all the habitats, except the flow oxbow lakes. Such a correlation was also observed for other representatives of Viviparidae. BUCKLEY (1986) and LEE et al. (2002) postulated that the age of female *V. georgianus* was a predictor of the size of the young and their future survival. A similar relationship was observed by RIBI & GEBHARDT (1986) for *V. ater*. In *V. viviparus* and *V. contectus* the female's size is not decisive for the size of the young. The neonates are wider than high (height 4.0 mm, width 4.5 mm) in females of all size classes (JAKUBIK & LEWANDOWSKI 2007). The female's size in these two species is a predictor of the proportion of embryos at various development stages – the largest females contain the greatest proportion of oldest embryos with developed shells (JAKUBIK 2007).

According to CALOW (1978), semelparous species under unfavourable habitat conditions risk the loss of many of their offspring, while iteroparous species can refrain from reproduction. In the studied iteroparous Viviparidae from the flow lakes earlier reproduction appeared to be the optimum survival strategy. The

question arises: which factors trigger the earlier reproduction as an adaptation to habitat conditions?

The food availability could be the first factor. Intensive feeding of the snails should follow the increased content of organic matter. The favourable food conditions in the flow lakes resulted from sedimentation of organic matter. The sedimentation rate varied seasonally, being higher in the spring than in the autumn (PORĘBSKI 2006), due to the floods and delivery of riverine organic matter. The spring floods of the Bug River (in March or April), which usually subside at the beginning of June, cause flushing and hence decrease of phytoplankton quantity. This could be the reason for the intensive feeding at the beginning of the vegetation season, when the snails exploited the elevated concentrations of organic matter, but were forced to switch to algal food in the summer and autumn (STAŃCZYKOWSKA et al. 1972). Such unstable food availability could result in earlier reproduction.

In variable habitats many snail species adopt a different strategy. The freshwater semelparous prosobranch *Bithynia graeca* lives in an artificial Lake Kerkini in northern Greece where the water volume and depth change very rapidly (ELEUTHERIADIS & LAZARIDOU-DIMITRIADOU 1995). *B. graeca* is adapted to the water level fluctuations: it has a high net reproduction coefficient and growth coefficient. Its short life cycle, high reproductive effort and the investment of energy into reproduction, as well as rapid growth under favourable conditions made it possible for the species to succeed in the specific habitat of Lake Kerkini.

Viviparidae in the oxbow lakes reproduced early but their life cycle did not shorten, as was shown in a field experiment (JAKUBIK & LEWANDOWSKI 2007). Additional evidence for this comes from shell thanatocoenoses found in the littoral zone of oxbow lakes (JAKUBIK unpublished) and formed as a result of e.g. strong wave action. Numerous thanatocoenoses were noted in the spring and summer due to the spring flooding and summer settlement of shell material. Similarly, washed up shells were observed by ALEXANDROWICZ (1999) in the littoral zone of Lake Gardno.

The ratio of empty shells and dead snails (shells with decaying bodies) to live snails in the flow lakes was small and constituted ca. 10%. This finding confirms the results of JURKIEWICZ-KARNKOWSKA (2006), who found empty viviparid shells in only two out of the 21 surveyed oxbow lakes of the Bug River. Empty shells and dead viviparids represented mainly size class III and fewer – class IV (Fig. 21A, B). Shells of other size classes contributed only a few percent. The size structure of empty shells and dead snails was similar to that

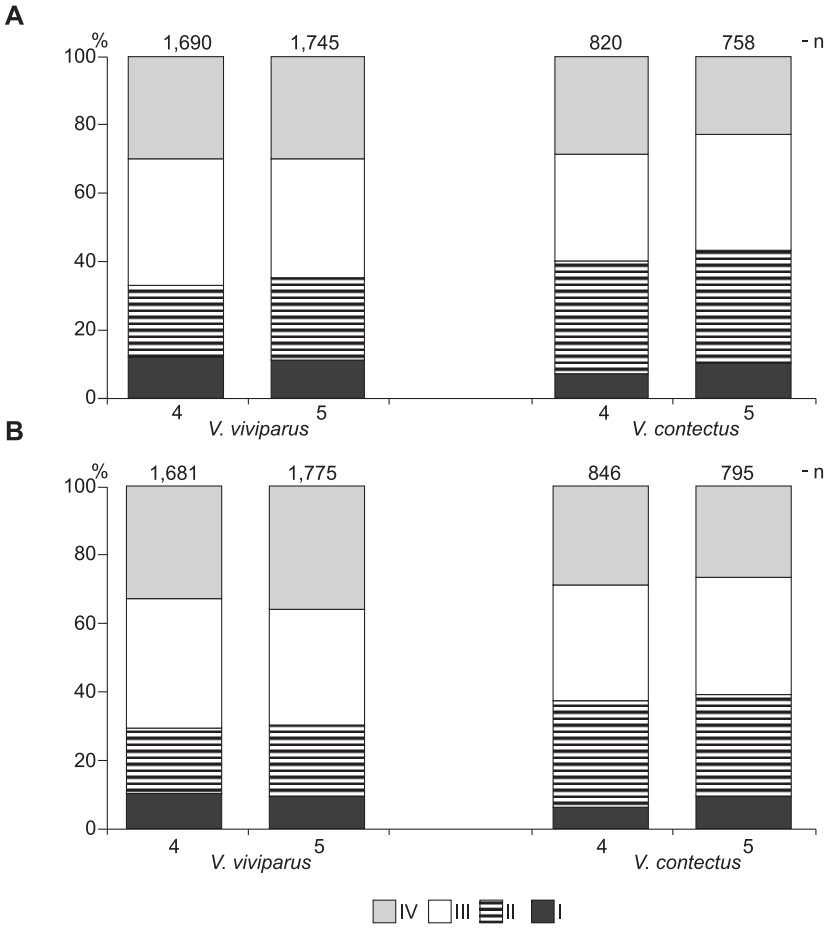

Fig. 21. Comparison of size structure (II–IV) of dead individuals (A) and empty shells (B) of *V. viviparus* and *V. contectus* in flow (4) and isolated (5) oxbows; mean values of 2003–2008

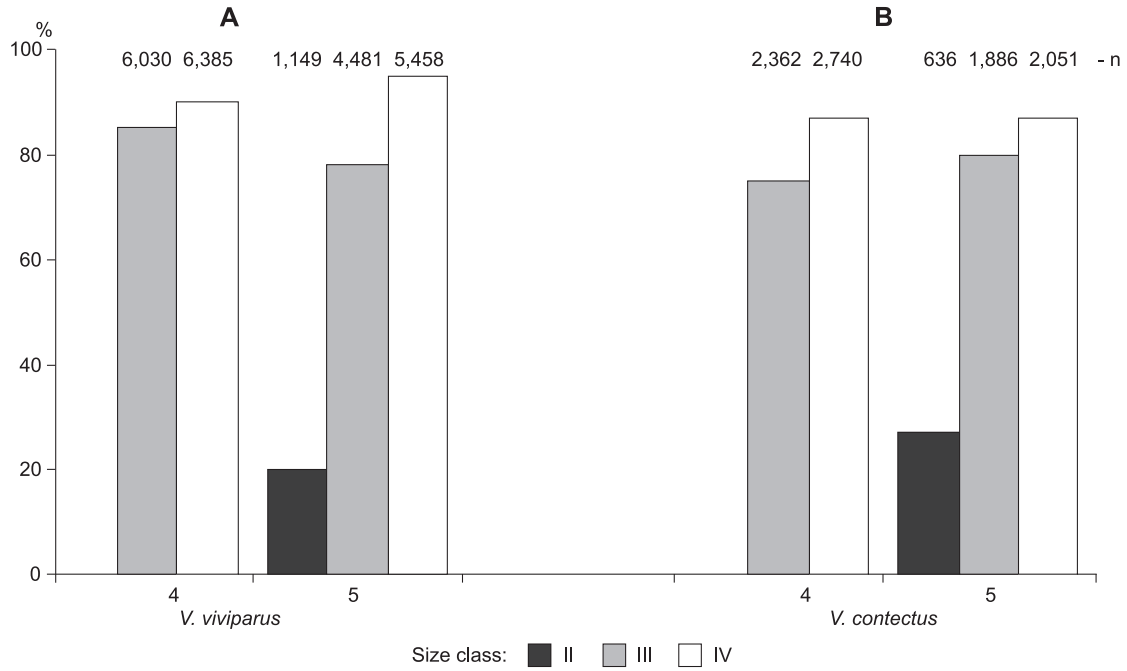

Fig. 22. Comparison of size structure (I–IV) of female *V. viviparus* (A) and *V. contectus* (B) infected with digenetic trematodes, from flow (4) and isolated (5) oxbows; mean values of 2003–2008

of live snails (Figs 6, 8). Since the phenomenon pertains to all size classes, probably the environmental factors rather than life cycle affect the mortality.

The early reproduction may also have resulted from infection by trematode cercariae. The extensity of infection of Viviparidae varies across Poland. WIŚNIEWSKI (1958) estimated it as 6.1% (23 trematode species found in snails) in the region of the Great Masurian Lakes (NE. Poland). In southwestern Poland BERTMAN & WOJCIECHOWSKA (1974) found 23 species of trematodes in *V. viviparus* and the extensity of infection was estimated as 36.6%. According to the literature data, trematode infection may limit fecundity in many snail species or preclude reproduction, probably because of castration of the host (JOKINEN 1982, MOURITSEN & JENSEN 1994, PROBST & KUBE 1999, SORENSEN & MINCHELLA 2001).

SAMOCHWALENKO & STAŃCZYKOWSKA (1972) observed an over 50% infection by trematode larvae in *V. fasciatus* and 30% in *V. viviparus* from Lake Czerniakowskie, Lake Mikołajskie and from the Narew and Krutynia rivers. Similar results for *V. viviparus* were obtained by NIKITINA (1986) in Lake Glubokoye, Russia, where 48% of the population were infected and by IVASUK (2005) in Lake Babje (28% infected) and in the Desna River (46% infected), Ukraine. JEŻEWSKI (2004) reported from 7% (Zegrzyński Reservoir) to 31% (Lake Mojtyńskie, Masurian Lakeland) infected individuals of *V. viviparus*. The respective values for *V. contectus* ranged from 10% (Lake Mokre) to 14% (Lake Czos).

The extensity of infection by trematode larvae in the studied flow oxbow lakes was high and exceeded 90%. A similar extensity was noted in the isolated lakes (Tukey test, p=0.85). The infected individuals represented only size classes III and IV; no parasites were found in snails of classes I and II. In the flow lakes, however, the parasites were found in snails of class II in both viviparid species. The proportion of infected snails in these classes was, however, distinctly smaller than in classes III and IV (Tukey test, p<0.001) (Fig. 22A, B).

Greater intensity of infection in older individuals may result from their larger size (BROWN et al. 1988, SNYDER & ESCH 1993) whereas the greater prevalence of trematodes among older and thus larger snails may be the effect of longer time available for infection. SAMOCHWALENKO & STAŃCZYKOWSKA (1972) noted a similar extensity of infection of female *V. viviparus* and *V. fasciatus* of size classes II, III, and IV, probably due to the short study period lasting from May till September.

Three species of trematodes: *Amblosoma exile*, *Neocanthoparyphium echinatoides* and *Leucochloridiomorpha lutea* were found in snails from the two types of oxbow lakes. The number of species is comparable with those reported in the literature. SAMOCHWALENKO & STAŃCZYKOWSKA (1972) recorded infection of *V. viviparus* and *V. fasciatus* by representatives of two families: Xiphidiocercarae and Echinostomatidae and by larvae of *Diastomum luteum*. JEŻEWSKI (2004) noted infection of *V. viviparus* and *V. contectus* from the Zegrzyński Reservoir and from the Wieprz and Narew rivers by six species of trematodes (*A. exile*, *N. echinatoides*, *L. lutea*, *Paracoenogonimus ovatus*, *Cercaria vesiculosa*, *Cercaria pugnax*). IVASIUK (2005) found *Leucochloridiomorpha constantinae* and *Cercaria bolschwensis*, and rediae of the subfamily Echinostomatidae in *V. viviparus* from the Kaniv and Babje dam

reservoirs on the Dnieper, while KRASUTSKA (2006) in the same area found *V. viviparus* to be infected by two species of trematodes (*L. constantinae, C. bolschwensis*).

N. echinatoides and *A. exile* were the most commonly found trematodes in the studied viviparids (90% and 80%, respectively); *L. lutea* was the least frequent. Infected and uninfected females from the flow lakes did not differ in fecundity (Tukey test, p=0.87). The mean numbers of embryos per uninfected and infected female of *V. viviparus* were 16.7 and 14.4, respectively. A similar lack of differences was found in *V. contectus*, with the mean values of 14.0 and 12.0 embryos per uninfected and infected female, respectively. These results suggest no effect of digenetic trematodes on the viviparid fecundity, contrary to the above mentioned literature data. A possible reason for such conclusion was the form of parasite (metacercariae) living in the snails. A similar phenomenon was observed by ŻBIKOWSKA (2006) in *Lymnaea stagnalis* infected by *Echinopatyphium aconiatum*. The trematode occurred in the form of metacercariae which affect snails to a lesser extent. This would explain the negligible effect of infection on the fecundity of Viviparidae which were infected by metacercariae alone. Parallel observations carried out in the isolated lakes did not show any decline in the viviparid fecundity. Studies by SAMOCHWALENKO & STAŃCZYKOWSKA (1972) on two viviparid species demonstrated, however, that the trematode infection decreased the fecundity of infected females by two to four times. The authors found metacercariae, cercariae, furcocercariae, rediae and sporocycts in the snails' bodies. Such diversity of invasive forms of the parasites could decrease the snails' fecundity.

Analyses of the relationships between the mean number and growth stage of embryos and the degree of infection showed a significant correlation only between the number of oldest embryos (juveniles with shells) of *V. viviparus* and the presence of *N. echinatoides* ($r=0.35$, $n=757$, $p<0.001$). The small correlation coefficient indicates that factors other than the trematodes were responsible for 88% variation in the growth of embryos.

It seems, therefore, that the reproduction is of the greatest importance for shaping viviparid populations. This is closely associated with the ovoviviparity of these snails since it allows for controlling the reproduction. Some features of reproduction in the populations of *V. viviparus* and *V. contectus* are flexible and adjustable to habitat conditions.

Viviparidae display two life strategies:

1. Individuals which mature later and attain maturity at large body sizes, and whose reproduction intensity increases with size are favoured; they guarantee maintaining a relatively stable population density. Young snails invest in growth and adults – in reproduction. Such a strategy was found in snails from the dam reservoir, ecotone habitats, rivers and isolated oxbow lakes.
2. In very variable habitats (e.g. flow oxbow lakes) Viviparidae start their reproduction early, when in size class II. Their reproduction effort is not correlated with their body size. Young viviparids invest in reproduction, as do the older ones. In this way they increase the chance for maintaining populations in such habitats.

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