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SIZE STRUCTURE, AGE, MORTALITY AND FECUNDITY IN *VIVIPARUS VIVIPARUS* (LINNAEUS, 1758) (GASTROPODA: ARCHITAENIOGLOSSA: VIVIPARIDAE)

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ABSTRACT: Field and laboratory experiments were aimed at establishing the relationship between growth rate, age, mortality and fecundity of *Viviparus viviparus* (L.). Fecundity was found to depend on the female's size. The size (shell dimensions) did not affect the size of newborn snails; females of different size classes produced offspring of the same shell height (4.0 mm) and width (4.5 mm). In the first year of the experiment growth rate was higher in the field than in the laboratory. Sex could be recognised and developing embryos could be found in females in the middle of the second year of the experiment. Juvenile *V. viviparus* appeared in the laboratory when the females were 18 months old and had achieved size class III. Their shell increments were uniformly distributed, without visible dark winter rings or rings of summer growth inhibition. Winter and summer rings appeared in the second year in the field culture; the second winter ring appeared in the third year of field culture. In the field females at the end of their second year contained embryos; they produced offspring in the spring of the third year.

KEY WORDS: *Viviparus viviparus*, fecundity, size structure, age structure, growth rate, mortality

INTRODUCTION

Body size and growth rate are important for the functioning of any organism; they affect the chances of survival and producing offspring, accumulation and allocation of energy reserves. At a certain optimum age, often regarded as equivalent to an optimum body size, the individual stops growing and starts reproducing. It depends on environmental conditions and life strategy (physiological lifetime, growth rate, number of offspring per brood, size of offspring, duration of particular stages of parental care, semelparity vs. iteroparity).

Freshwater snails usually attain sexual maturity before they finish their growth (FRETTER & GRAHAM 1962, BUCKLEY 1986, STAŃCZYKOWSKA & LEWANDOWSKI 1995, LEWANDOWSKI 1996, 2001, LEWANDOWSKI et al. 1997, ELEUTHERIADIS & LAZARIDOU-DIMITRIADOU 2001, CZARNOŁĘSKI et al. 2003, 2005). The same is sometimes true of terrestrial gastropods (WIKTOR 2004): the reproductive organs of larger individuals may be less developed than those of smaller animals (UMIŃSKI 1975, JACKIEWICZ & ZBORALSKA 1994, JACKIEWICZ 2003) and the largest individuals at the end of their life show a smaller fecundity (VALECKA & JÜTTNER 2000).

Viviparus viviparus (L.) is a common bottom-dwelling snail in freshwater habitats of Poland. It is iteroparous, dioecious and sexually dimorphic. Based on annual growth rings various authors (WESENBERG-LUND 1939, FRÖMMING 1956, SPOËL 1958, STAŃCZYKOWSKA 1960) have estimated its lifespan as 5–10 years.

STAŃCZYKOWSKA (1960) has proposed an age-related 4-grade size scale for *V. viviparus*. Class I includes snails aged 0 to one month. Snails of class II are one to several months old. *Viviparus* born in the spring or summer overwinter as class II individuals and attain the size of class III in the second year of life. In their third or fourth year the snails attain the size of class IV. Since the pertinent literature was published in the first half of the 20th c., we decided to verify the age and size data. The relationship between growth rate and age is crucial for the interpretation of fecundity and mortality. Whether individuals of a new generation attain maturity and reproduce in the year of their birth also depends on the growth rate of young snails.

The experiment was aimed at: 1. estimating fecundity of females in various size classes; 2. comparing mortality of females in various size classes and of their offspring; 3. estimating the growth rate of individuals of the new generation since birth; 4. verifying the hypothesis that the snails do not reproduce in the year of their birth.

STUDY SITE

The study was carried out in an oxbow lake Wywłoka situated in the Bug River Valley Landscape Park (Fig. 1). The lake is c. 20 ha in area and has a maximum depth of 3.5 m. In the 1980s it was divided by a dike equipped with culverts. The western part of the lake opens to the river, resulting in unstable habitat conditions caused by spring floods and inflow of suspended matter from the river. In the site *V. viviparus* is accompanied by *V. contectus*.

METHODS

A hundred females of *V. viviparus* were randomly collected in the lake during the reproductive period. Nets, drags and sieves used to collect and wash the material had the mesh size of 1 mm. The snails were divided into size classes based on shell height and width measured with calipers to the nearest 0.1 mm (STAŃCZYKOWSKA 1960). Class I included young individuals with characteristic hairy shells and shell height not exceeding 8.0 mm. Snails of class II had shells of height and width ranging from 8.1 to 12.0 mm. The shell width in class III ranged from 12.1 to 20.0 mm, the height – from 12.1 to 25.0 mm. Individuals with shells of width and height within 20.1–25.0 and 25.1–35.0 mm, respectively, were included in class IV (Fig. 2).

Twenty females of each size class were placed separately in an aquarium of 30 l volume, water temperature c. 23°C, regularly aerated. The snails were fed

Fig. 1. Oxbow lake Wywłoka

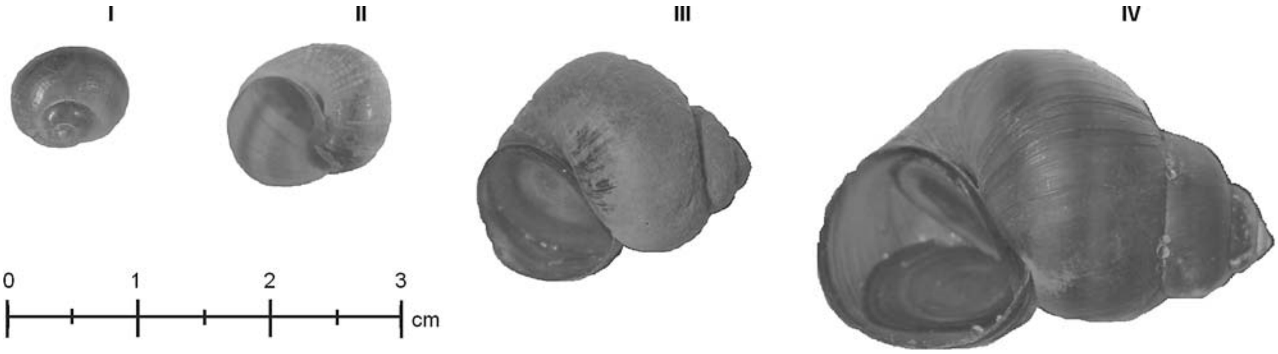

Fig. 2. Four size classes of *V. viviparus*

with detritus and aquarium fish food. An additional culture was kept to maintain a stable density in the experimental aquaria in cases of high mortality.

Fecundity (expressed as the number of produced juveniles) was recorded for each size class one day after placing the females in aquaria and then every week during four subsequent weeks. Mortality of females and juveniles, as well as the number of surviving juveniles were also recorded. Live juveniles were transferred to separate aquaria according to the size classes of their mothers. During one year their shell height and width were measured monthly, to the nearest 0.1 mm with a calibrated eyepiece. Additionally, rings on the shell and operculum were counted and potential fecundity was assessed.

The field experiment was run in parallel to the laboratory culture. One hundred females were caught at random in the oxbow lake Wywłoka during the reproductive period. The snails were divided into classes according to their size and placed in four marked cages 30 × 15 × 45 cm made of plastic net (mesh size 1 cm) (Fig. 3). The net allowed for free water flow but prevented the escape of young and adult snails.

The cages were checked for juveniles (fecundity estimate) one day after placing the snails there and then once a week during four subsequent weeks. Mortality was estimated one week after the culture started. Newborn snails and dead females were removed from the cages and counted. Shell height and width of juveniles were measured and the snails were placed in new cages according to the females' size class. The juvenile shells were measured once a month for 24 months, with winter breaks between the 7th and 11th (November 2003–March 2004), and between the 19th and 23rd (November 2004–March 2005) month. During winter (November till March) the cultures were unavailable for observation. Rings on the shell and operculum were counted and potential fecundity was assessed.

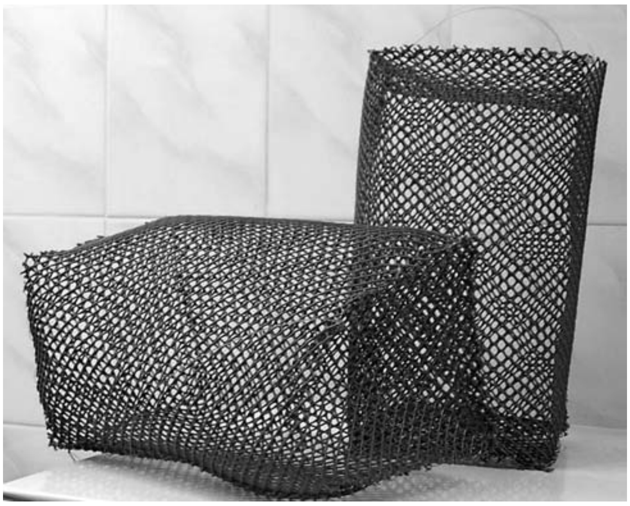

Fig. 3. Experimental cages

Statistical analyses were performed with Statistica for Windows 3.11 (ŁOMNICKI 1995).

RESULTS

After the first day of laboratory experiment juveniles were found in aquaria with females of classes III (mean 3.8 juvenile per female) and IV (mean 4.3) (Fig. 4). Females of class II produced offspring in the first week of observations (mean 2.7 per female). In the second, third and fourth weeks of observations the fecundity in all size classes decreased to 2 juveniles per female, except class II females which did not produce offspring in the fourth week.

Most juveniles produced at the beginning of observations (on the first day) were offspring of the biggest females of classes III (40%) and IV (60%). This could be explained by greater fecundity typical in *V. viviparus* of these size classes. In the field the fecundity was smaller than in the laboratory. The smallest females of class II produced offspring only in the first and second weeks, those of classes III and IV – during the entire month.

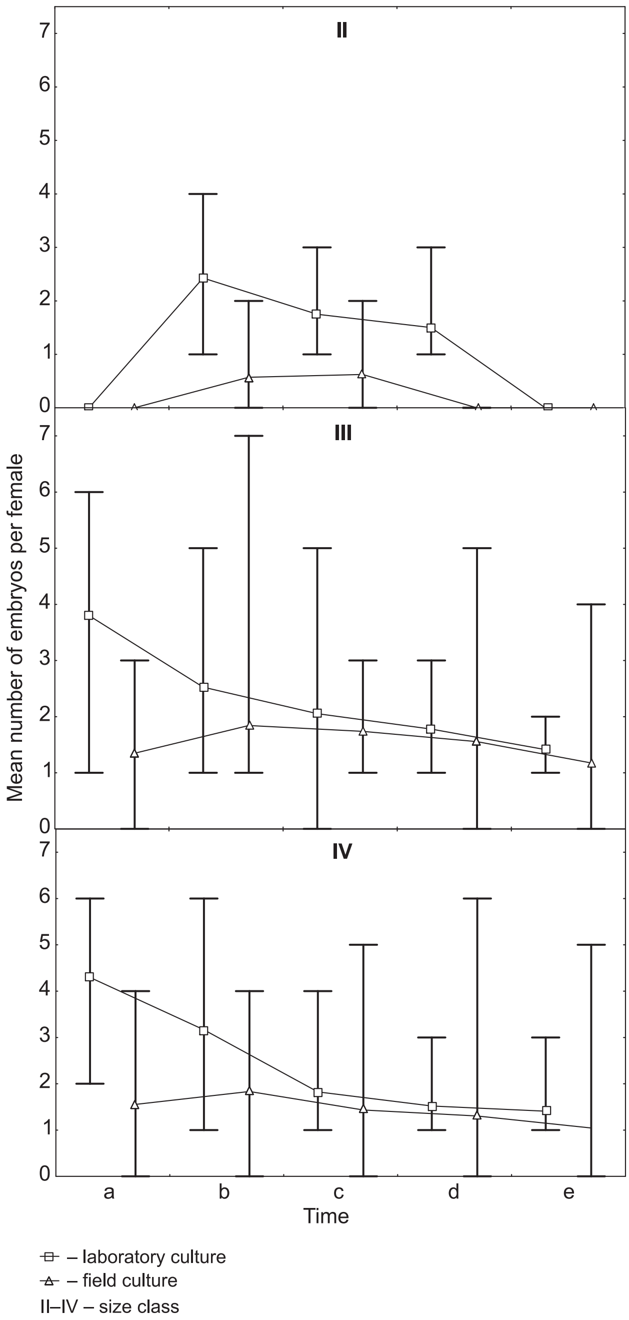

Fig. 4. Mean number of embryos per female in size classes from laboratory and field cultures (a – day, b – 1 week, c – 2 weeks, d – 3 weeks, e – 4 weeks)

On the first day of laboratory observations the mortality among class II females was 60% and among those of classes III and IV – 30% (Fig. 5A). In the field the mortality was markedly higher than in the laboratory. Mortality of young *V. viviparus* varied with time. For offspring produced by class II females the second week was critical and then the mortality reached 62% (Fig. 5B).

At birth the shells of the juveniles were wider than high and were of the same size (4.0 mm high, 4.5 mm wide) for all size classes of the mothers. After one month of life in the laboratory the shell height was 4.5 mm for all snails and the width increased by 0.1 mm in the offspring of class II mothers, by 0.2 mm in that of class III mothers and by 0.3 mm in that of class IV mothers. The shells of snails aged one month were almost as wide as they were high; the height and width did not differ significantly ($t=15.56$, $df=243$, $p=0.62$). Shell increments were similar for all snails till the end of the first year of life ($t=26.02$, $df=1024$, $p=0.76$) irrespective of the size class of their mothers ($r^2=0.03$, $p<0.05$) (Fig. 6A). In the second month the shell width and height increased by 0.8 mm and in the third – by 0.9 mm. Between the fourth and sixth months of life the shell height increased by 0.7 mm and the width – by 0.8 mm per month. In the sixth month the snails reached the size of class I (shell width and height over 8.0 mm) and in the tenth month – of class II. Shells of snails aged one year were 14.0 mm high and 14.2 mm wide (Fig. 6A). The snails did not produce offspring in the first year of life. In the second year the shell height increased faster than the width ($t=44.11$, $df=542$, $p<0.001$) (since the age of 13 months – May 2004) (Fig. 6A). In the middle of the second year it was possible to distinguish sex and find developing embryos in the oviducts of females. Juveniles appeared when the females attained the age of 18 months (October 2004). The shell increments were uniform, without dark winter rings or rings of summer growth inhibition.

The size of snails aged one month in the field was the same as in the laboratory, and did not depend on the size class of the mothers ($r^2=0.04$, $p=0.75$). In the next month the increments of shell height ($t=44.12$, $df=58$, $p<0.001$) and width ($t=28.91$, $df=64$, $p<0.001$) were very high (c. 10 mm) and the snails reached the size of class II; they retained the same size until cessation of field observations (sixth month) in the first year (Fig. 6B). The shell height and width increased by c. 0.8 mm per month but the width increments were slightly faster than those of the height ($t=36.82$, $df=32$, $p<0.001$). In the second year of field culture a thick, dark winter ring appeared on the shells. It could be seen in 85% of all individuals at the mean shell width 14.2 mm and mean height 17.2 mm (Table 1). This inhibition was also marked as an additional ring on the operculum. In the second year the shells reached the size of class III. The growth was probably continued in the late autumn of the preceding year and in the early spring of the next year (when weather conditions made observations impossible). In the second year of observations a ring of summer growth inhibition was found in 20% individuals. At the end of that year 64% individuals had such a ring. It was present in snails of the mean width of 17.7 mm and the mean height of 22.0 mm. In the 24th month (April 2005) of the culture the second winter ring appeared. It was recognisable in 72% individuals with the mean shell width 18.3 mm and height 23.8 mm. Some

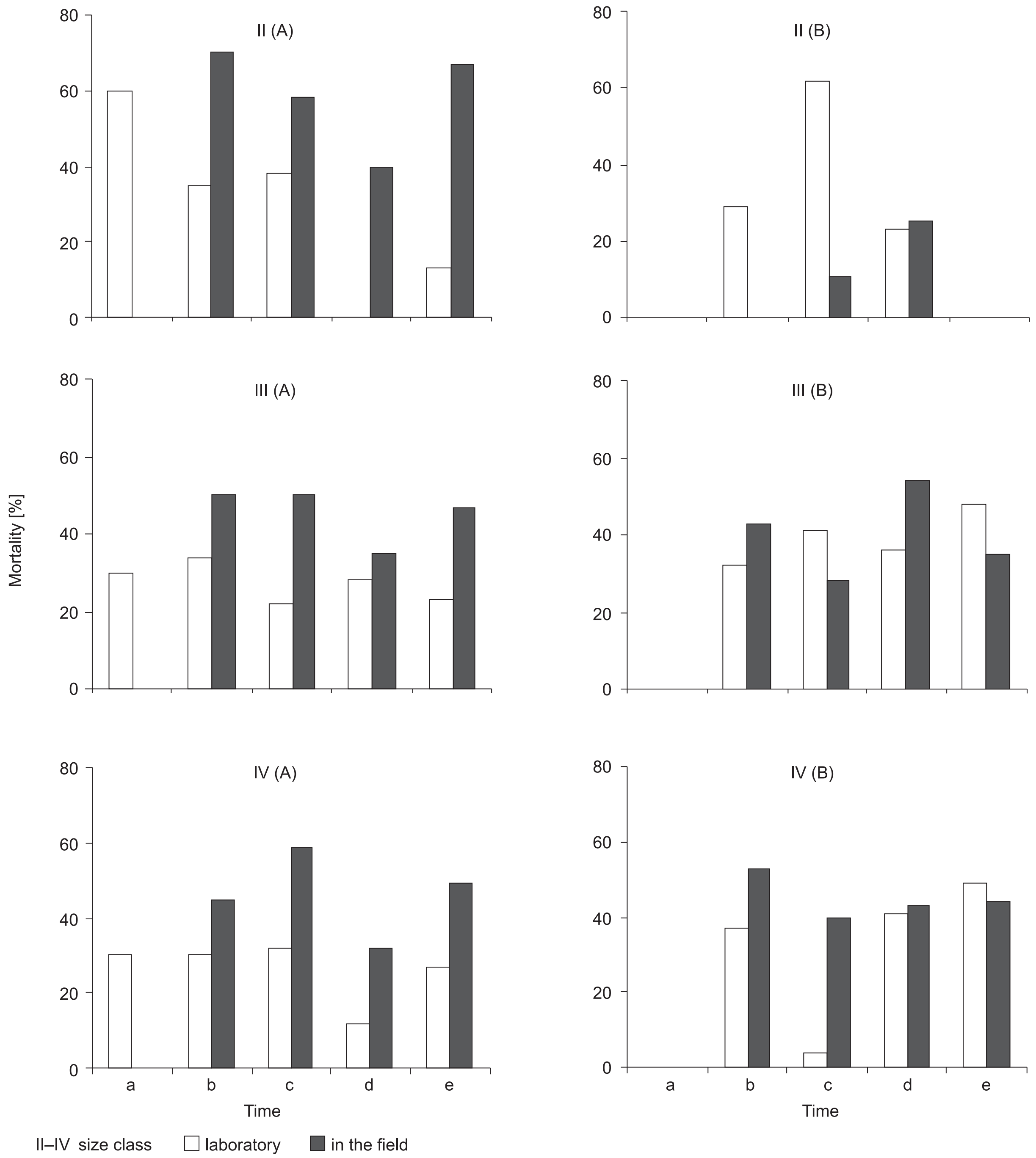

Fig. 5. Mortality of females (A) and juveniles (B) of *V. viviparus* in individual size classes in the laboratory and in the field (a – day, b – 1 week, c – 2 weeks, d – 3 weeks, e – 4 weeks)

Table 1. Growth rings in snails from the field culture [mean values ± S.D. (minimum–maximum) are given]

Year	1st winter ring		summer ring		2nd winter ring	
	shell height (mm)	shell width (mm)	shell height (mm)	shell width (mm)	shell height (mm)	shell width (mm)
1						
2	17.2 ± 1.86 (13.0–19.7)	14.2 ± 1.48 (11.4–17.3)	22.0 ± 2.11 (14.5–24.0)	17.7 ± 1.42 (12.2–20.0)		
3					23.8 ± 1.37 (14.2–24.0)	18.3 ± 1.05 (14.2–24.0)

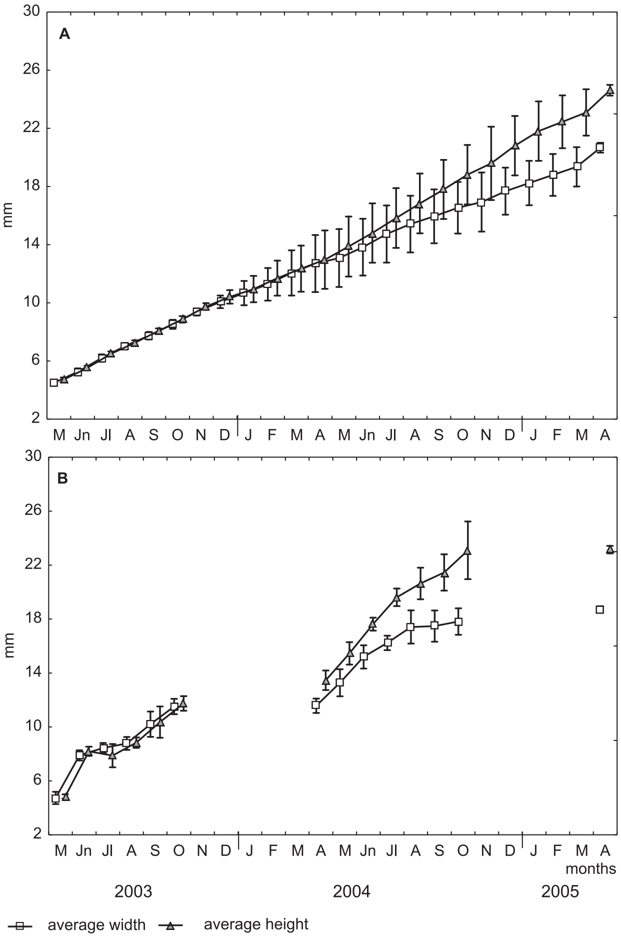

Fig. 6. Shell height and width increments in the laboratory (A) and in the field (November–March without shell increments) (B)

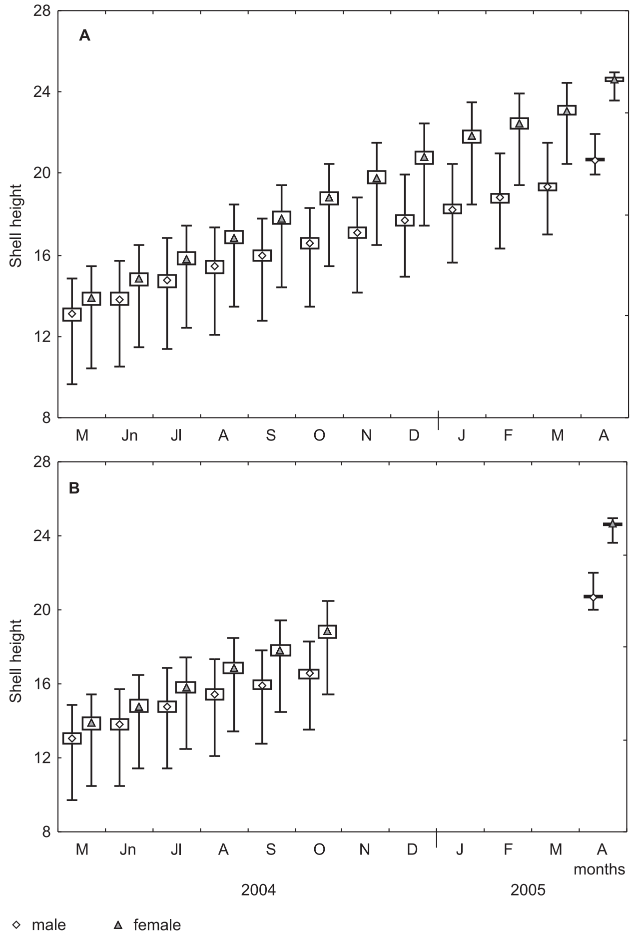

Fig. 7. Comparison of shell height increments in females and males of *V. viviparus* in the laboratory (A) and in the field (November–March without shell increments) (B)

(18%) snails had only one winter ring and 10% had none. The second winter growth inhibition was marked as additional rings on the operculum.

Differences similar to those observed in the laboratory were found in the rate of shell growth. The shell height increased definitely faster than width ($t=28.91$, $df=64$, $p<0.001$). At the end of the second year embryos were found in the oviducts. In the 24th month (April 2005) of life the snails produced offspring.

It was possible to estimate sex ratio when the snails reached the size of class II (shell width and height >8.0 mm). Since the shell height increased faster than the width in individuals of that class, the shell height was used in further comparisons. In both laboratory and field cultures the shell size increased with females' ($r^2=0.93$, $p<0.05$) and males' ($r^2=0.94$, $p<0.05$) age (Fig. 7A, B). The height increments differed between the sexes ($t=10.25$, $p<0.001$). The shell height was slightly higher in females both in the laboratory culture ($t=8.52$, $p<0.001$) and in the field ($t=9.49$, $p<0.001$), compared to males. The differences in shell size between the sexes did not affect the number of growth lines on the shell and operculum.

DISCUSSION

The female body size has a significant effect on fecundity in the population of *V. viviparus*. A relationship between fecundity and age (expressed as body size) has been also observed in other viviparids: *Viviparus georgianus* (BUCKLEY 1986), *V. viviparus* (JAKUBIK 2006) or *V. ater* (RIBI & MUTZNER-WEHRLI 1987).

The female size in *V. viviparus* does not affect the size of its offspring, contrary to what is often observed in other viviparids. All juveniles had the same shell size at birth. BUCKLEY (1986) has found a correlation between the size of *V. georgianus* females and juveniles within each age class. He has also noted marked differences in shell height and biomass of offspring produced by females of different age classes. No such relationships were found in the studied population of *V. viviparus*. The growth rate was the same in all young *V.*

viviparus regardless of their mother's size. In the population of *V. viviparus* the individual growth rate depends on age, interactions between the sexes and environmental conditions (in the case of field culture). In *V. georgianus* the growth rate of the youngest snails has been found to decrease with age and size. The most intensive growth takes place during the first 5–6 months. In *V. viviparus* intensive growth at the beginning of the season was observed only in the field cultures (Fig. 6). In the laboratory population size increments were even as a result of stable culture conditions. These conditions (no predators, water currents etc.) resulted in a lower mortality of females, compared to those from the lake. The juvenile mortality did not show such pattern. Since the size of offspring does not depend on the female's size in *V. viviparus*, the mortality of juveniles and females may not depend on body size as has been observed by BUCKLEY (1986) for the population of *V. georgianus*. This question needs further detailed studies on mortality of *V. viviparus* over a longer period. In snails whose shell does not develop continuously there are periods of intensive growth alternating with periods of rest. In unfavourable environmental conditions, when the shell growth is impeded, characteristic black rings, called winter rings, are formed which enable estimating the mollusc age (e.g. LEWANDOWSKI 1983, 2001). The distance between two such rings represents one year. The rings have been repeatedly used to estimate the age of viviparids (e.g. SPOËL 1958, STAŃCZYKOWSKA 1960, DE BERNARDI et al. 1976a, b, BROWNE 1978). The estimated age ranges from 2 to 11 years. The wide range of reported life spans is a result of semelparity or iteroparity of various species and of different habitat conditions. The life span of *V. contectus* is 4 years (SAMOCHWALENKO & STAŃCZYKOWSKA 1972), that of *V. ater* – 3–10 years (BARBATO 1971, RAVERA et al. 1972, RIBI & ARTER 1986). The life span reported for the English population of *V. viviparus* is 2 years (YOUNG 1975), for the Polish population 5–10 years (PIECHOCKI 1979), for the Dutch population – as long as 11 years (SPOËL 1958). Corresponding estimates for the Canadian population of *Viviparus malleatus* are over 5 years (STAŃCZYKOWSKA et al. 1971) and for the population of *V. georgianus* in the US – 2 to 4 years (BROWNE 1978, VAIL 1978, JOKINEN et al. 1982, JOKINEN 1985, BUCKLEY 1986, TESSIER et al. 1994).

The age estimates are not always precise because rings might be due to other reasons (PIECHOCKI 1979, FALNIOWSKI 1989). The age estimate in *V. viviparus* based exclusively on winter and summer rings is accurate in the case of young individuals (up to the third year). In older viviparids the borders between rings become obliterated, moreover, the shells of older individuals are worn, making accurate counting difficult. Counting is also difficult in the case of dark brown, violet or completely black shells. For these reasons age estimates should be supplemented with observations on the size structure, particularly when the ring identification is uncertain. In the latter case the age estimate can be based on the similarity of shells when the individual growth rate is known.

SPOËL (1958) based his age estimates in *V. viviparus* on the shell height, width and on the maximum number of winter rings. He found that the usual life span of *V. viviparus* was 6 years, though snails aged 11 years could also be found. The first winter ring appeared at the shell height of 8.0 to 19.0 mm. These data are consistent with the values obtained in the present study in the field culture. The range of shell heights refers to class II which is attained in the first year of the snail's life. The first ring appears at the shell height falling within the range of class II and III in the culture i.e. in the second year of life. The second ring refers to class II and the remaining rings (third to sixth) – to class IV. It thus appears that the first size class includes snails aged from one to several months which in the middle of the year grow up to the second size class. That class comprises snails one year old. In the second year the snails have one winter ring and in the middle of that year grow to the size of class III. Sex can be recognised in the second year. The second winter ring appears in the third year of life and the snails attain the size of class IV. The size classes distinguished by STAŃCZYKOWSKA (1960) should be supplemented with the estimate based on winter rings and extended to include class V, i.e. snails in the fourth and fifth years of life. Apart from regular winter rings, summer rings of growth inhibition should be considered. They might indicate the occurrence of random unfavourable conditions, such as rapid drop in water temperature, water level or changes in other physical and chemical environmental factors. The summer rings are also associated with reproduction, i.e. growth inhibition due to investment of resources in reproduction. During that period the resources are allocated to the production of gametes which results in a limited growth of somatic tissues. This was confirmed by the appearance of the summer ring in *V. viviparus* not earlier than in the second year in the field culture, when the snails attained class III and produced progeny at the beginning of the third year. In freshwater molluscs the energy allocation has been found to vary with age (BROWNE & RUSSELL-HUNTER 1978, TASHIRO 1982, RUSSELL-HUNTER & BUCKLEY 1983). In very sensitive molluscs the so-called alarm rings may be produced. Such rings have been reported for *Dreissena polymorpha* by KACHANOVA (1963) and LEWANDOWSKI (1983). The rings appeared in bivalves in culture after measurements of their shell lengths. We did not observe such rings in *V. viviparus*. The viviparid shell closes with the operculum which grows together with the shell, the growth being manifest as concentric increments that should be also considered when estimating age (FALNIOWSKI et al. 1997).

V. viviparus attains sexual maturity in the second year of life. In the same year it may reproduce. According to FRÖMMING (1956) Viviparidae in Central Europe attain maturity in the second year but more than 90% females do not yet contain embryos. The individual size in *Viviparus* is critical for the reproductive activity. It is often determined by such habitat factors as food quality which has been demonstrated for *Cipangopaludina chinensis*, *Viviparus fasciatus* and *V. viviparus* by STAŃCZYKOWSKA et al. (1972). Intraspecific differences in shell size might affect the age at first reproduction which was shown in this paper.

Our experiment showed that the snails did not reproduce in the year of their birth. Though the size of juvenile *V. viviparus* is not determined by the body size of their mothers, that size determines the fecundity and the number of embryos as has been demonstrated earlier (JAKUBIK 2006, 2007). There is a positive correlation between the mean number of embryos and shell height, shell width, dry body weight and dry weight of the female's shell. The number of embryos in particular growth stages is also associated with these biometrical indices. The mean number of the oldest embryos (fully developed snails with shell) increases with the increase in shell height and width and dry weight of female *V. viviparus*. The dry body weight of the female is most closely correlated with the number of embryos at the youngest growth stage (oval, transparent egg capsules).

The results of this experiment show that age classes are not equivalent to size classes in *V. viviparus*. It means that a snail of class II is not always 2 years old. This is especially important when estimating and comparing the reproductiveness of several populations of *V. viviparus*. A lack or small proportion of class II females containing embryos is a result of their young age. When females of that class do reproduce it is usually in response to specific environmental conditions.

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