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ON THE REPRODUCTION OF *PISIDIUM* C. PFEIFFER, 1821 (BIVALVIA: SPHAERIIDAE) FROM SĄPOLNO (NW. POLAND)

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ABSTRACT: During a malacofaunistic survey in the environs of Sąpolno (Pomeranian Lakeland, NW. Poland) 16 species of *Pisidium* were found within an area of 2.5×2.0 km: *P. amnicum* (O. F. Müller), *P. casertanum* (Poli), *P. crassum* (Stelfox), *P. globulare* Clessin, *P. henslowanum* (Sheppard), *P. hibernicum* Westerlund, *P. milium* Held, *P. moitessierianum* Paladilhe, *P. nitidum* Jenyns, *P. obtusale* (Lamarck), *P. personatum* Malm, *P. ponderosum* (Stelfox), *P. pseudosphaerium* Schlesch, *P. pulchellum* Jenyns, *P. subtruncatum* Malm and *P. supinum* A. Schmidt. The number of offspring during the reproductive season depended on the species and on the parent's size. The most fecund species was *P. ponderosum*, with up to 75 juveniles released at once. The offspring of *P. amnicum* were the largest (mean shell length 2.05 mm), but relatively small compared to the parent's shell (mean 26.1%). The smallest juveniles were produced by *P. moitessierianum* (mean shell length 0.59 mm). The juvenile shells of the studied species were more or less elongated, with the height/length ratio ranging from 0.75 (*P. amnicum, P. ponderosum, P. henslowanum*) to 0.83 (*P. subtruncatum, P. hibernicum*). Distinct differences were observed in the reproduction of *P. casertanum* and *P. ponderosum*. However the differences between the reproductive parameters of *P. ponderosum* and the form described as *P. casertanum* var. *humeriformis* were rather small.

KEY WORDS: ovoviviparity, fecundity, infra-specific differences, shell of offspring

INTRODUCTION

Bivalves of the genus *Pisidium* C. Pfeiffer, 1821 are ovoviviparous hermaphrodites. Their embryos develop in brood pouches formed by ctenidia (only one pouch at a time) (MEIER-BROOK 1970, HOLOPAINEN & HANSKI 1986, PIECHOCKI 1991, KORNIUSHIN 2007, PIECHOCKI & WAWRZYNIAK-WYDROWSKA 2016). When the embryos are shell-covered, the pouch walls burst but the juveniles remain within the parent's body for some time and continue growing (PIECHOCKI 1991, KORNIUSHIN 2007). Only after they have been released, new pouches with new embryos can be formed.

Among the pisids the biology of *P. amnicum* is the best known (e. g. ODHNER 1929, DANNEEL & HINZ 1976, MEIER-BROOK 1977, BASS 1979, HOLOPAINEN 1979, VINCENT et al. 1981, HOLOPAINEN & HANSKI 1986, PIECHOCKI & DYDUCH-FALNIOWSKA 1993, HOLOPAINEN et al. 1997, RANTANEN et al. 1998, ARAUJO et al. 1999, MOUTHON & DAUFRESNE 2008, PIECHOCKI & WAWRZYNIAK-WYDROWSKA 2016). Comparison of observations of different populations of the species shows how widely the life cycle parameters (e.g. growth rate, course of reproduction, life span) vary under the effect of climate conditions (HOLOPAINEN & HANSKI 1986, ARAUJO et al. 1999, MOUTHON & DAUFRESNE 2008). Similar variation pertains to other pisid species.

Nineteen species of the genus *Pisidium* occur in Poland (PIECHOCKI & SULIKOWSKA-DROZD 2008, PIECHOCKI & WAWRZYNIAK-WYDROWSKA 2016) and all of them have been reported from the Pomeranian Lakeland (NW. Poland) (TETENS & ZEISSLER 1964, PIECHOCKI 1989, WŁOSIK-BIEŃCZAK 1992b, PIECHOCKI & DYDUCH-FALNIOWSKA 1993, PIECHOCKI 2002). When the studies were done in the central part of the region (Fig. 1), I found 16

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species within an area of 2.5×2.0 km: *Pisidium amnicum* (O. F. Müller, 1774), *P. casertanum* (Poli, 1791), *P. crassum* (Stelfox, 1918), *P. globulare* Clessin, 1873, *P. henslowanum* (Sheppard, 1823), *P. hibernicum* Westerlund, 1894, *P. milium* Held, 1836, *P. moitessierianum* Paladilhe, 1866, *P. nitidum* Jenyns, 1832, *P. obtusale* (Lamarck, 1818), *P. personatum* Malm, 1855, *P. ponderosum* (Stelfox, 1918), *P. pseudosphaerium* Schlesch, 1947 (often erroneously cited as Favre, 1927), *P. pulchellum* Jenyns, 1832, *P. subtruncatum* Malm, 1855 and *P. supinum* A. Schmidt, 1851.

MATERIAL AND METHODS

The material was collected in 1997–1999 in the environs of the village Sąpolno (Fig. 2). The bivalves were identified based on shell characters according to PIECHOCKI & DYDUCH-FALNIOWSKA (1993). In order to avoid mistakes, individuals with atypical shells (e.g. misshapen or intermediate between species) were disregarded. The shells left as voucher material were additionally verified with the key of GLÖER & MEIER-BROOK (2003). Based on anatomical differences some authors divided the genus *Pisidium* into an array of subgenera. Here I adopted the division used by GLÖER & ZETTLER (2005).

Adult bivalves (usually with shelled embryos visible through the shell) were kept in the laboratory

Figs 1–2. Location of the study area: 1 – general view, 2 – map of the environs of Sąpolno

till they released the offspring. Individuals which: (1) released offspring immediately after being placed in the culture, and the released juveniles were few (some may have been released in the field); (2) started releasing offspring only after a few months (unfavourable food conditions in the culture may have caused death of some embryos) were omitted from the fecundity data analysis. Small pieces of decaying tree leaves found in the water (mainly black alder, less often poplar or oak) and a small quantity of brown suspension from drainage ditches were placed in the containers as food. The bivalves were kept mostly singly, in containers of 25 mm diameter filled with water to 20 mm (rarely in groups, to collect a large number of juveniles). Only *P. amnicum* and the largest species: *P. casertanum, P. ponderosum* and *P. henslowanum* (shell length more than 4.5 mm), were kept in larger containers of 60 mm diameter and water 30 mm deep. When the observations were concluded, both the juveniles and most of the adults were released in their original sites. Only a part of the largest individuals of all the species were retained in the laboratory.

The shells were measured with calibrated eyepiece to the nearest 0.01 mm (size below 1 mm) or 0.05 mm (range 2.3–5.0 mm). Adult shells more than 5 mm long were measured on graph paper, magnification 6× (accuracy ca. 0.1 mm). Newly released juveniles were measured in a large drop of water; all the adult and juvenile *P. amnicum* were dried prior to measurements.

In the text "n" means the number of measured parents or offspring, r – Pearson's coefficient of linear correlation, SD – standard deviation. In the figures the numbering of water bodies (e.g. drainage ditches) is separate for each species.

RESULTS AND DISCUSSION

Pisidium (*Pisidium*) *amnicum* (O. F. Müller, 1774)

In the studied area the species occurred in the rivers Brda and Lipczynka. The largest found empty shell was 11.2 mm long. Four distinct growth inhibition striae were usually visible on shells of more than 10 mm (less often 3 striae). The first stria was marked at the shell length of 3.7–8.2 mm.

Adult individuals, collected in April–May and placed in the culture, released offspring in May. In the wild offspring release usually started at the beginning of May and finished in the second half of June. This conforms to the data on the populations from Germany and Great Britain (DANNEEL & HINZ 1976, MEIER-BROOK 1977, BASS 1979). In Spain and France juveniles appeared already in April (ARAUJO et al. 1999, MOUTHON & DAUFRESNE 2008), and in Canada and Finland they were released as late as in June or July (VINCENT et al. 1981, HOLOPAINEN & HANSKI 1986, RANTANEN et al. 1998).

The number of released offspring was correlated with the parent's shell length (r=0.73, n=14) (Fig. 3). In the culture the smallest offspring-releasing (7 young) individual had shell 5.2 mm long. The maximum number of offspring during one reproductive period was 46 (Table 1) and was similar to that reported by DANNEEL & HINZ (1976), BASS (1979) and KORNIUSHIN (2007). In the countries with warmer climate it was higher, with the maximum values: in Spain 73 (ARAUJO et al. 1999), and in France even 163 juveniles produced by one parent (MOUTHON & DAUFRESNE 2008).

At the moment of release the juveniles had shells 0.92–2.78 mm long (mean 2.05 mm, SD=0.35, n=229) (Fig. 4). The smallest offspring with shells of 0.92–1.17 mm came from one parent (the smallest, shell 5.2 mm long). The remaining individuals produced larger offspring (more than 1.35 mm in length). The shell height/length ratio was 0.707–0.787 (mean 0.748, SD=0.016, n=168). The offspring reached on average 26.1% of the parent's shell length (SD=4.5, n=229, range 14.7–42.2%). The literature data on the juvenile shell length vary from 1.8–2.2 mm (DANNEEL & HINZ 1976, MEIER-BROOK 1977, BASS 1979, VINCENT et al. 1981, HOLOPAINEN & HANSKI 1986) to 2.7 mm (ODHNER 1929, PIECHOCKI & DYDUCH-FALNIOWSKA 1993).

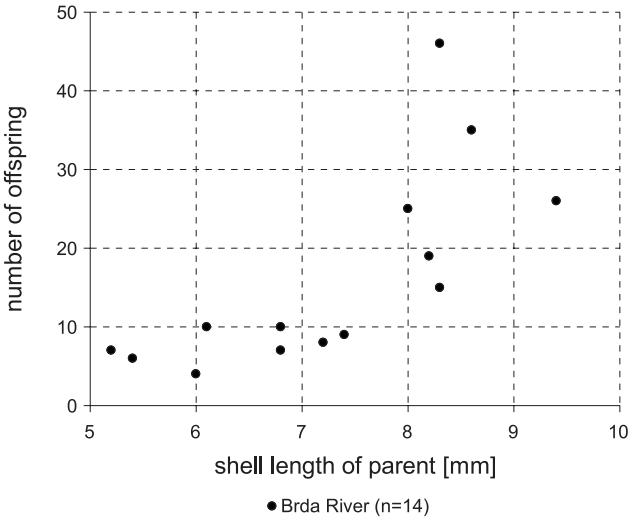


Fig. 3. *Pisidium amnicum*: parent size and number of offspring

Table 1. Genus *Pisidium*: maximum number of offspring released in one reproductive period

Species	Parent's shell length [mm]	Period of offspring release	Number of offspring	Shell length of released young [mm]	
				min–max	mean
P. amnicum	8.30	May	46	1.52–1.93	1.68
P. casertanum	4.48	June	37	1.13–1.27	1.20
P. globulare	3.40	March	23	1.03–1.13	1.07
P. ponderosum	4.28	May–June	75	0.53–0.94	0.77
P. var. *humeriformis*	4.48	May–June	75	0.78–0.94	0.89
P. personatum	2.85	May	10	0.99–1.10	1.04
P. obtusale I	3.38	June	26	0.92–1.12	1.00
P. obtusale II	3.70	July	26	0.78–0.86	0.83
P. hibernicum	2.58	July	19	0.70–0.80	0.75
P. milium	3.10	June	18	0.97–1.17	1.08
P. pseudosphaerium I	3.08	June	17	0.92–1.03	0.95
P. pseudosphaerium II	3.13	June	17	0.92–1.03	0.98
P. nitidum	3.38	June	35	0.77–0.88	0.83
P. crassum I	2.97	May	30	0.76–0.88	0.82
P. crassum II	3.24	May	30	0.78–0.95	0.88
P. subtruncatum	3.52	May	45	0.73– 0.85	0.80
P. pulchellum	3.98	June	22	1.17–1.33	1.24
P. henslowanum	4.90	June	58	0.74–0.97	0.88
P. supinum	3.66	June	46	0.70–0.97	0.80
P. moitessierianum I	1.95	April	21	0.51–0.59	0.56
P. moitessierianum II	1.95	May	21	0.55–0.62	0.58

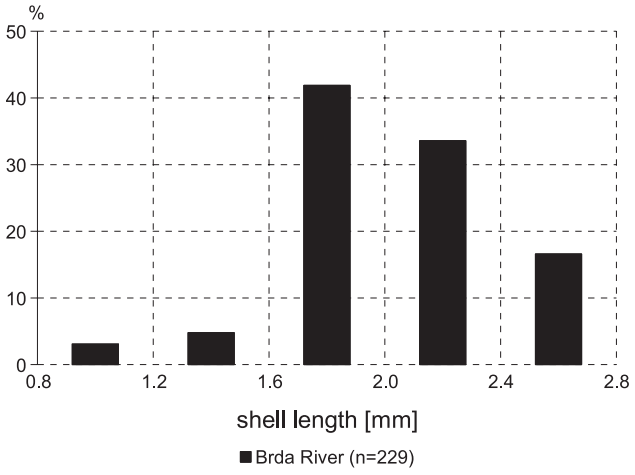


Fig. 4. *Pisidium amnicum*: shell length variation among offspring

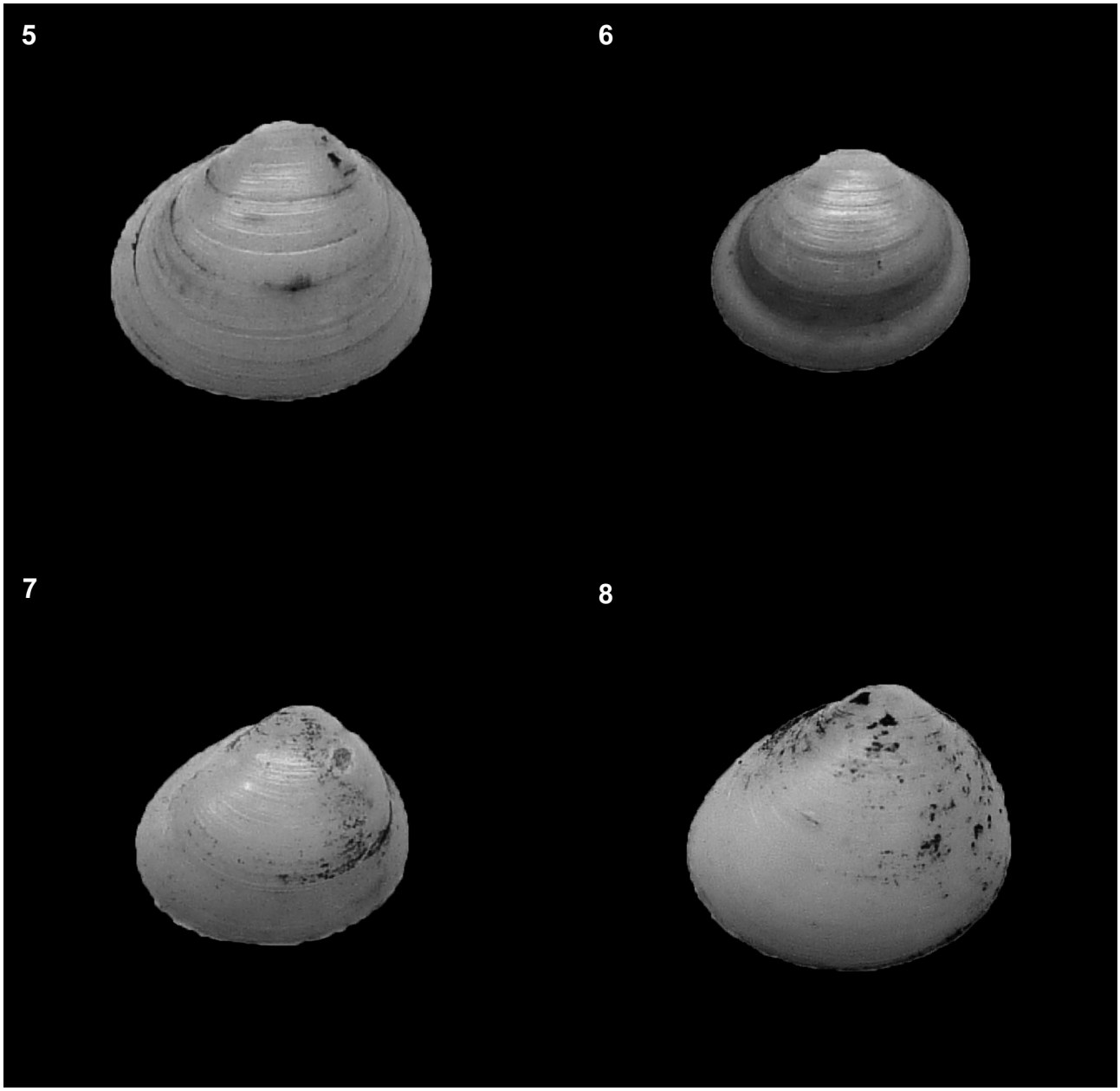
Pisidium (*Euglesa*) *casertanum* (Poli, 1791)

The species occurred in drainage ditches, shallow oxbows and fens (on some wet meadows). Most of the sites were permanently under water (even during drought). Figures 5–8 present typical shells of *P. casertanum, P. globulare, P. ponderosum* and *P.* var. *humeriformis*, which till recently were regarded as conspecific. Shells of *P. casertanum* were mostly oval, with moderately protruding and rather wide umbones (Fig. 5). In some populations the shell walls were thick and the hinge plate wide, in others the walls were relatively thin and the plate narrow.

Adults with shelled embryos were found from May till July (sporadically also in August). When placed in the laboratory, they usually released offspring in June and July (rarely as early as the end of May, or in August). The literature data on the timing of offspring release vary widely: April–June (Burky et al. 1981), June–July (Hamill et al. 1979), June–November (Mackie 1979), July (Heard 1965, Holopainen 1979), or November–December (Holopainen & Jónasson 1983).

The number of released offspring was correlated with the parent's shell length (r=0.65, n=99) (Fig. 9). In the culture the smallest offspring-releasing (2 young) bivalve had shell 2.41 mm long. The maximum number of offspring during one reproductive season was 37 (Table 1), in another two populations it was 34 and 30, respectively. However, only three individuals were so fecund, the remaining ones produced not more than 22 juveniles. In the literature a similar number of offspring (42) was reported by Heard (1965), while populations studied by other authors were less fecund (Mackie 1979, Holopainen & Jónasson 1983, Piechocki & Dyduch-Falniowska 1993).

When released, the juveniles had shells 0.78–1.79 mm long (mean 1.24 mm, SD=0.16, n=2,120) (Fig. 10). The populations varied much in this respect. The smallest juveniles (mean length 1.09 mm) were produced by the bivalves from the fast-flowing ditch parallel to Lipczynka River (1st in Figs 9–10). The largest offspring (mean length 1.34 mm) was that of the



Figs 5–8. Shells of *Pisidium casertanum* (5), *P. globulare* (6), *P. ponderosum* (7) and *P.* var. *humeriformis* (8); left valve, 10×

bivalves from the small fen on the slope of the Brda valley (water outflow from a drain). In the remaining populations the mean shell length of offspring was: 1.23 mm (ditch draining Lake Sosnowe – 2nd in Fig. 9) and 1.25 mm (drainage ditch on meadows near Lake Mosyny – 3rd in Fig. 9). The height/length ratio was mostly 0.74–0.78 (mean 0.760, SD=0.021, n=1,714, range 0.683–0.833) (in the studied populations the mean values varied from 0.753 to 0.771). The offspring reached on average 32.5% of the parent's shell length (SD=5.3, n=1,082, range 19.5–59.2%). The shell length reported by other authors was within 0.8–1.3 mm (HAMILL et al. 1979, HOLOPAINEN 1979,

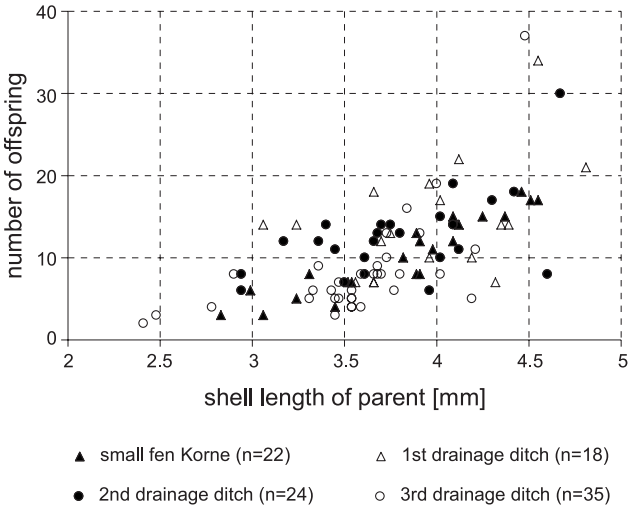


Fig. 9. *Pisidium casertanum*: parent size and number of offspring, divided into studied populations

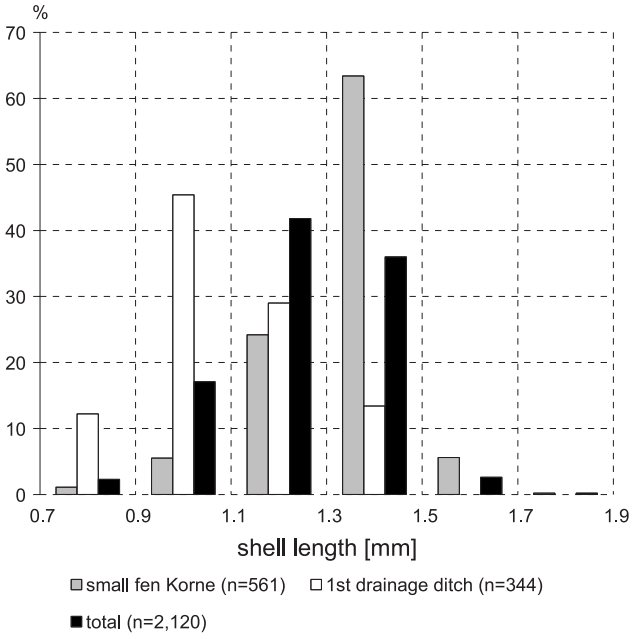


Fig. 10. *Pisidium casertanum*: shell length variation among offspring (total) and 2 examples of variation in populations

MACKIE 1979, BURKY et al. 1981, HOLOPAINEN & JÓNASSON 1983, PIECHOCKI 1983, HOLOPAINEN & HANSKI 1986, PIECHOCKI & DYDUCH-FALNIOWSKA 1993, PIECHOCKI & WAWRZYNIAK-WYDROWSKA 2016).

Pisidium (*Euglesa*) *globulare* Clessin, 1873

The species occurred mainly in shallow, initial sections of some drainage ditches (sometimes very abundantly). The bivalves spent dry periods in the layer of damp leaves or in the mud. However, at high water level (e.g. during local floods) they moved to the surrounding meadows. The shells were strongly convex, with wide umbones protruding above the upper margin (Fig. 6). The shell walls were relatively thin, with very numerous pores, which agrees with KORNIUSHIN's data (1999).

In the wild, throughout the year (including winter) a part of individuals contained shelled embryos. When placed in the culture, usually in a short time they released offspring. In the wild the time of release was limited by both the temperature and the water level (the temperature and water level usually permitted offspring release from the end of April till September, with irregular breaks).

The number of offspring was poorly correlated with the parent's shell length (r=0.52, n=134) (Fig. 11). In the culture the smallest offspring-releasing (2 young) bivalve had shell 2.30 mm long. The maximum number of offspring in one reproductive period was 23 (Table 1), in another two populations it was 21 and 17, respectively.

The new-born young had shells 0.80–1.91 mm long (mean 1.38 mm, SD=0.16, n=1,812) (Fig. 12). The mean shell length in the studied populations was 1.29, 1.35 and 1.43 mm. The smallest offspring came from the site with the greatest fecundity (ditch near Korne, 1st in Figs 11–12). The remaining sites were located in meadows near Sąpolno (2nd and 3rd ditches in Figs 11–12). The height/length ratio was usually 0.78–0.82 (mean 0.793, SD=0.024, n=1,698, range 0.707–0.859) (mean values for the populations: ditch near Korne – 0.770, ditches near Sąpolno – 0.802 and 0.798). The offspring reached on average 36.6% of the parent's shell length (SD=5.1, n=1,094, range 21.6–54.8%).

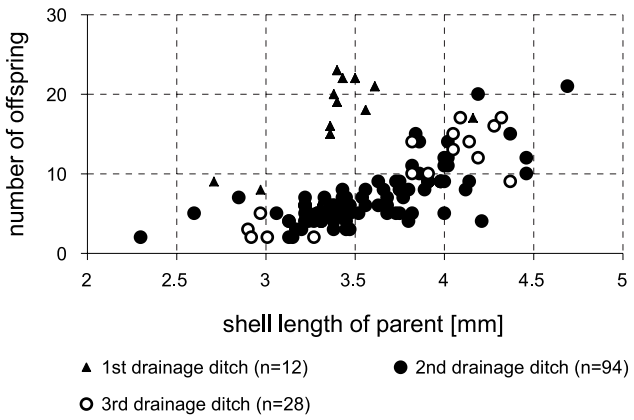


Fig. 11. *Pisidium globulare*: parent size and number of offspring, divided into studied populations

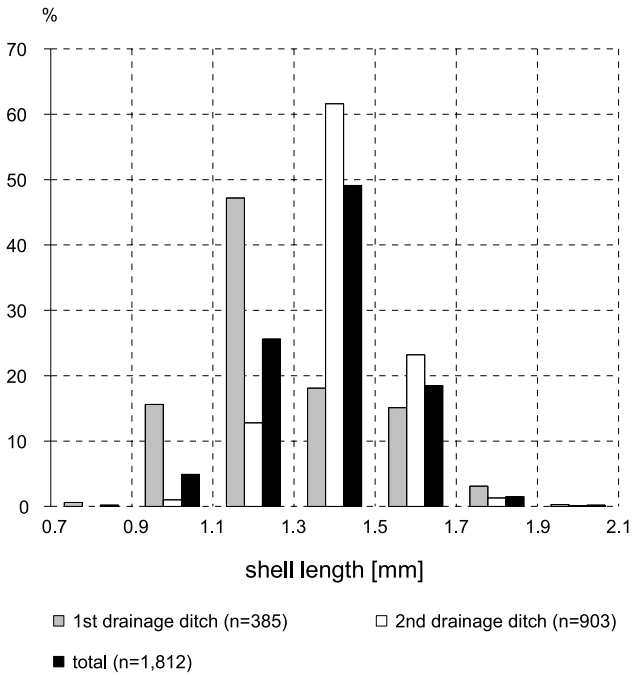


Fig. 12. *Pisidium globulare*: shell length variation among offspring (total) and 2 examples of variation in populations

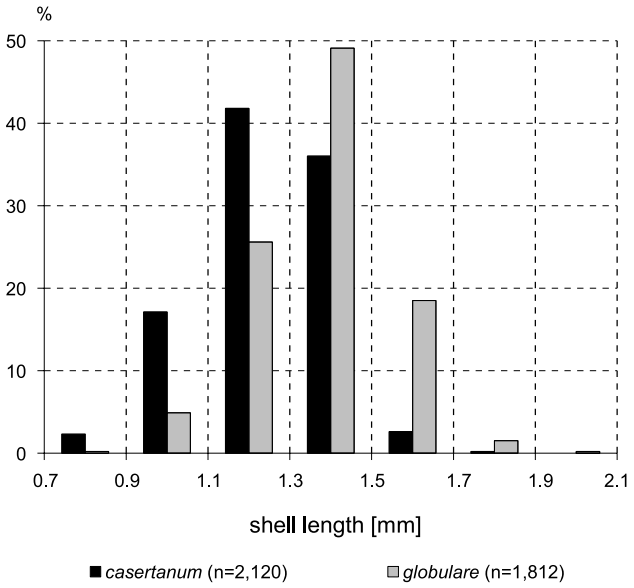


Fig. 13. Comparison of *Pisidium casertanum* and *P. globulare:* shell length variation among offspring

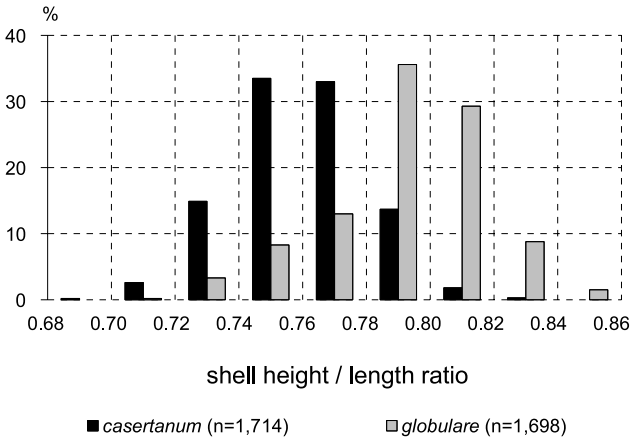


Fig. 14. Comparison of *Pisidium casertanum* and *P. globulare:* variation in shell proportions among offspring

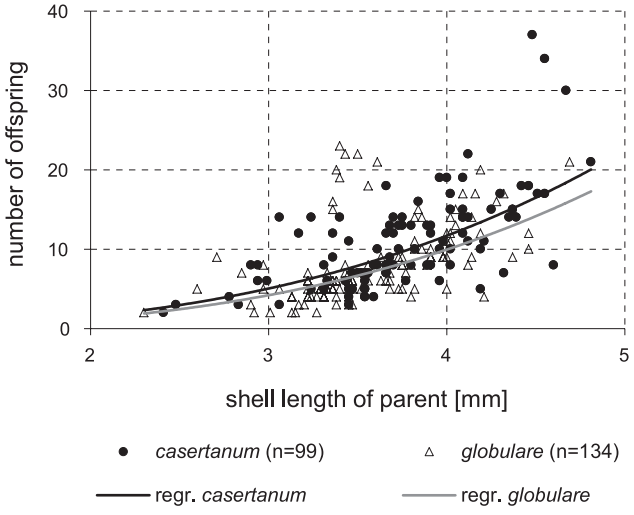


Fig. 15. Comparison of *Pisidium casertanum* and *P. globulare:* parent size and number of offspring

The shells of juvenile *P. globulare* were mostly somewhat larger compared to *P. casertanum*, but their variation ranges were similar (Fig. 13). However, the species differed rather distinctly in their shell proportions (Fig. 14). At the same length of parent's shell the mean number of offspring was slightly smaller in *P. globulare* than in *P. casertanum* (Fig. 15). For example, at shell length of 4 mm *P. globulare* produced on average 10 juveniles, and *P. casertanum* released 13 juveniles.

Pisidium (*Euglesa*) *ponderosum* (Stelfox, 1918) + var. *humeriformis* Stelfox

The taxonomic status of the bivalve described by STELFOX (1918) as *P. casertanum* var. *humeriformis* and var. *ponderosa* raised controversies from the very beginning. Some authors regarded the last variety as a distinct species, others as a variety or subspecies of the conchologically variable *P. casertanum*. Studies on shell variation seemed to confirm that it was a form of *P. casertanum* (e. g. KUIPER 1963, PIECHOCKI 1989, WŁOSIK-BIEŃCZAK 1992a). Ecological studies gave different results (MEIER-BROOK 1975, PIECHOCKI 1991, ZETTLER & GLÖER 2006). In recent publications *P. ponderosum* was treated as a distinct species, for example by GLÖER & ZETTLER (2005), PIECHOCKI & SULIKOWSKA-DROZD (2008), GLÖER & DIERCKING (2010), PIECHOCKI & WAWRZYNIAK-WYDROWSKA (2016). Both forms occurred in the studied area (Brda River and Lake Sosnowe), syntopically or separately. The shells of *ponderosa* were strongly convex, in outline close to triangular (the short upper margin was usually invisible in lateral view) (Fig. 7). The shells of *humeriformis* were moderately convex (sometimes even flattened), trapezoidal in outline, with narrow umbones protruding above the upper margin (Fig. 8). The largest collected shells of the two forms were ca. 5 mm long. The hinge plate was very wide, with massive lateral teeth A1 and P1 as well as A2 and P2. The shell surface in *ponderosa* was feebly shiny, in *humeriformis* usually matt. In *ponderosa* and in *humeriformis* from a sandy bottom the shell walls were thick, without pores. Individuals of the form *humeriformis* living among plant roots or on a muddy bottom had thinner shell walls with pores. According to KUIPER (1963) the boundary between the two forms was difficult to discern because of the existence of individuals with intermediate shell characters. In the study area only a few small specimens from the Brda River were difficult to assign to any form (those were disregarded in the analysis).

Adults of both forms collected in the spring, when placed in the culture, released offspring from half of May till half of June. In the wild, at the end of June only few adults contained shelled embryos and released them in July–August. The number of offspring

was closely correlated with the parent's shell length: in *ponderosa*: r=0.83, n=98; in *humeriformis*: r=0.90, n=45 (Fig. 16). In the culture the smallest offspring-releasing bivalves had shells: *ponderosa* – 2.62 mm long (5 young), *humeriformis* – 2.35 mm long (7 young). The maximum number of offspring in both forms was 75 (Table 1).

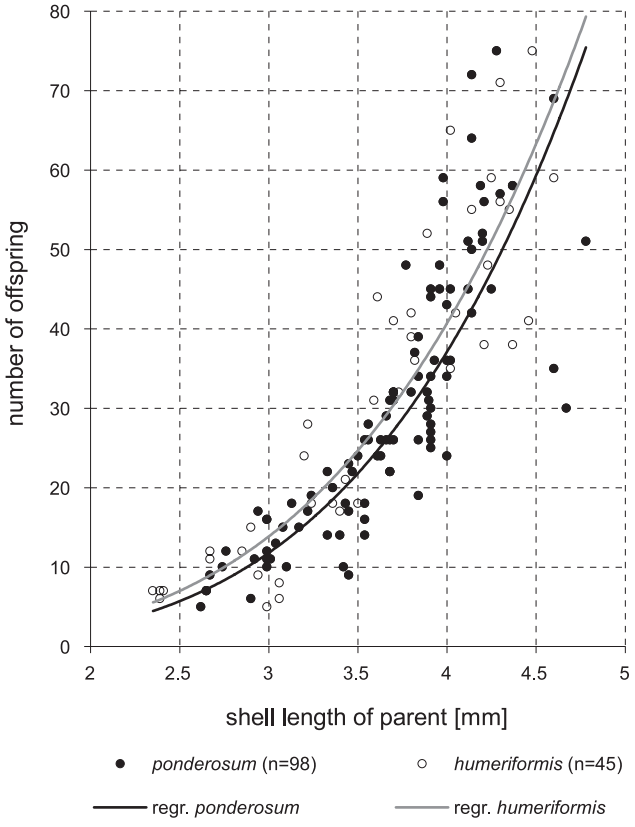


Fig. 16. *Pisidium ponderosum* and *P.* var. *humeriformis*: parent size and number of offspring

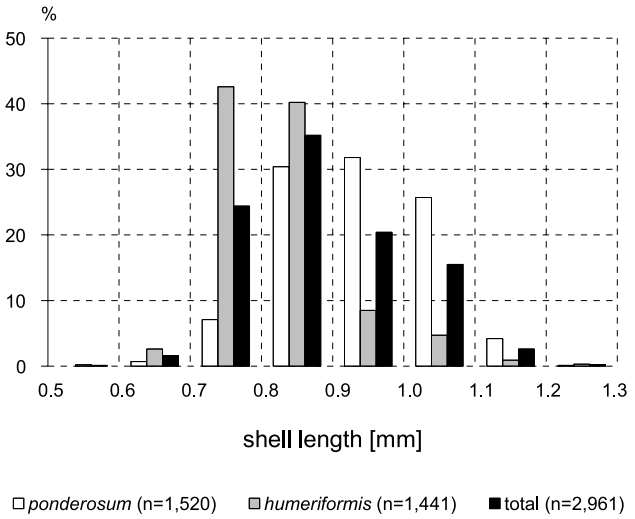


Fig. 17. *Pisidium ponderosum* and *P.* var. *humeriformis*: shell length variation among offspring

The remaining parameters of reproduction were the following. In *ponderosa* the length of juvenile shells was 0.57–1.26 mm (mean 0.94 mm, SD=0.10, n=1,520) (Fig. 17). In the river population the mean shell length was smaller than in the lake (0.87 and 1.00 mm, respectively). The height/length ratio was 0.679–0.806 (mean 0.748, SD=0.019, n=1,073); mean for the river 0.756, mean for the lake 0.743. The offspring reached 15.9–37.0% of the parent's shell length (mean 24.8 %, SD=3.9, n=1,520): for the Brda mean 21.8%; for Lake Sosnowe mean 27.0%.

In *humeriformis* the length of juvenile shells was 0.53–1.29 mm (mean 0.83 mm, SD=0.09, n=1.441) (Fig. 17). In the river population the shells were shorter than in the lake (mean length 0.81 and 0.96 mm, respectively). The height/length ratio was 0.677–0.814 (mean 0.752, SD=0.018, n=942); mean for the river 0.753, mean for the lake 0.749. The offspring reached 11.8–42.1% of the parent's shell length (mean 21.7%, SD=4.9, n=1,441): mean for the Brda 20.1%; mean for Lake Sosnowe 32.4%.

The relationship between the two forms (conchological forms or closely related species) remains unclear. On the one hand they differ in shell structure which makes it possible to distinguish between them (Figs 7–8), on the other their reproductive parameters are similar (Figs 16–17). Assuming that

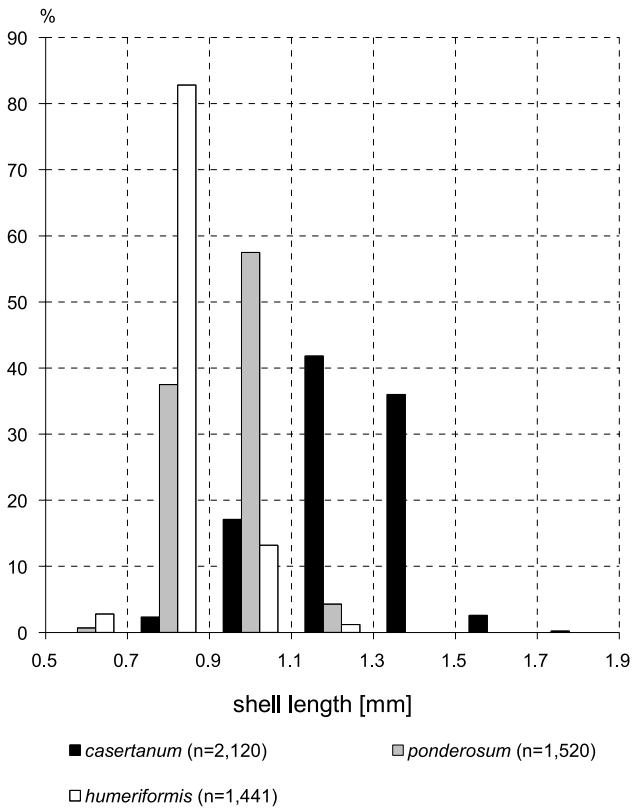


Fig. 18. Comparison of *Pisidium casertanum*, *P. ponderosum* and *P.* var. *humeriformis*: shell length variation among offspring

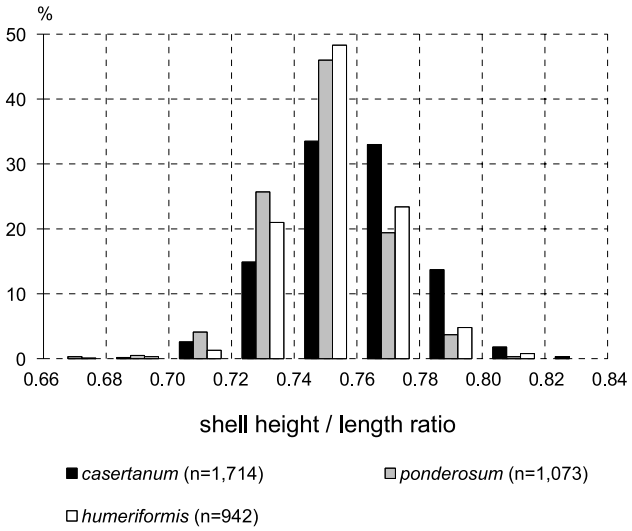


Fig. 19. Comparison of *Pisidium casertanum*, *P. ponderosum* and *P.* var. *humeriformis*: variation in shell proportions among offspring

the two forms are conchological extremes of *P. ponderosum*, the combined data would be: mean juvenile shell length 0.89 mm (SD=0.11, n=2,961) (Fig. 17); mean height/length ratio 0.750 (SD=0.017, n=2,015); mean relative size of offspring 23.4% of the parent's shell length (SD=4.8, n=2,961).

The juvenile shell length in both typical *P. ponderosum* (=var. *ponderosa*) and var. *humeriformis* was usually smaller than in *P. casertanum*, but the variation ranges overlapped partly (Fig. 18). The shell proportions were very similar (Fig. 19). At the same length of parent's shell the number of released offspring in *P. ponderosum* and var. *humeriformis* was usually 2–3 times greater than in *P. casertanum* (e.g. at 4 mm 38, 43 and 13, respectively) (Fig. 20). The offspring release in *P. ponderosum* and var. *humeriformis* was usually earlier than in *P. casertanum*.

Pisidium (*Euglesa*) *personatum* Malm, 1855

The species occurred in a few drainage ditches and in some springs on wet meadows. Adults with shelled embryos were found from April to August. Placed in the culture, they released offspring from April till November. In some individuals the period between release of the first and the last juvenile was relatively long (even up to 3 months). In the studied sites the number of offspring was small and poorly correlated with the parent's shell length (r=0.46, n=33) (Fig. 21). In the culture the smallest offspring-releasing (5 young) bivalve had shell 2.28 mm long. The maximum number of offspring in one reproductive period was 10 (Table 1), in another population 8. According to HEITKAMP (1980) and DYDUCH-FALNIOWSKA (1983), *P. personatum* has two reproductive periods per year.

On release, the offspring had shells 0.80–1.43 mm long (mean 1.08 mm, SD=0.12, n=298) (Fig. 22). The mean shell length in the studied two populations was 1.09 mm (ditch near Sąpolno) and 1.07 mm (ditch near Korne). The height/length ratio was 0.707–0.814 (mean 0.758, SD=0.021, n=298) (mean values in the populations: ditch near Sąpolno – 0.750, ditch near Korne – 0.767). The offspring on average reached 39.4% of the parent's shell length (SD=4.9, n=167, range 25.0–52.1%).

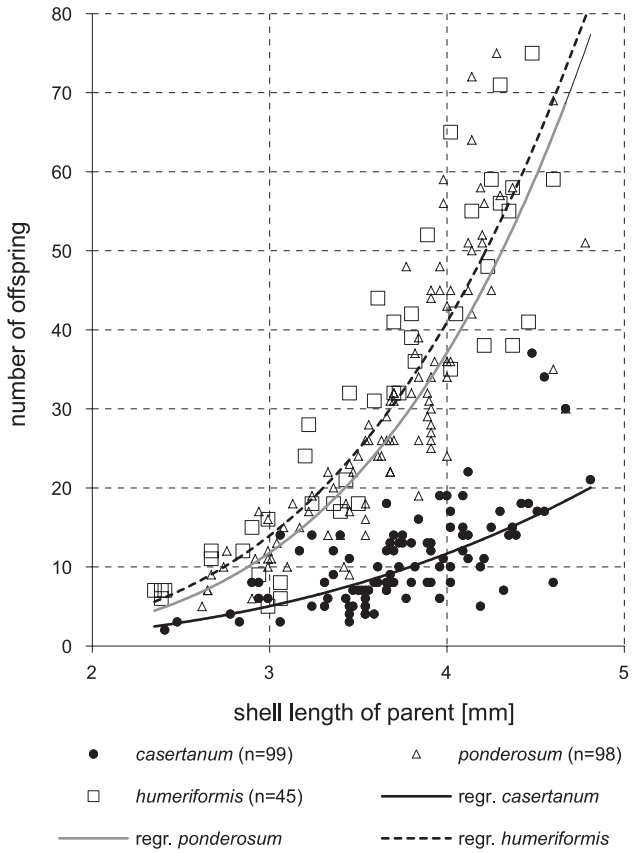


Fig. 20. Comparison of *Pisidium casertanum*, *P. ponderosum* and *P.* var. *humeriformis*: parent size and number of offspring

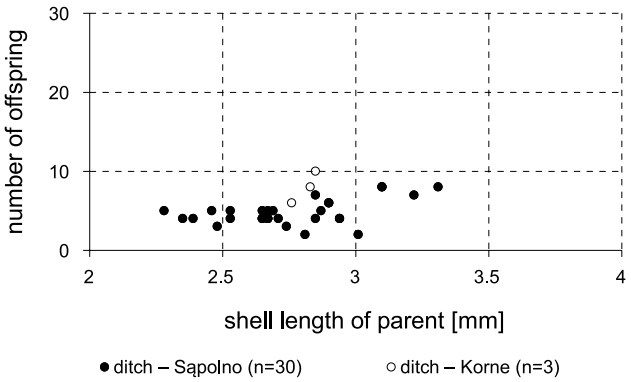


Fig. 21. *Pisidium personatum*: parent size and number of offspring, divided into studied populations

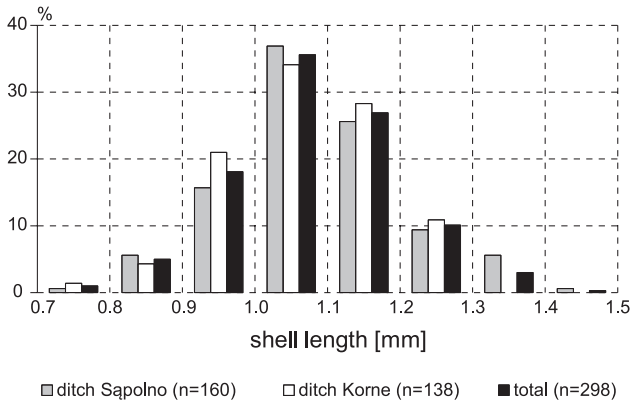


Fig. 22. *Pisidium personatum*: shell length variation among offspring (total) and 2 examples of variation in populations

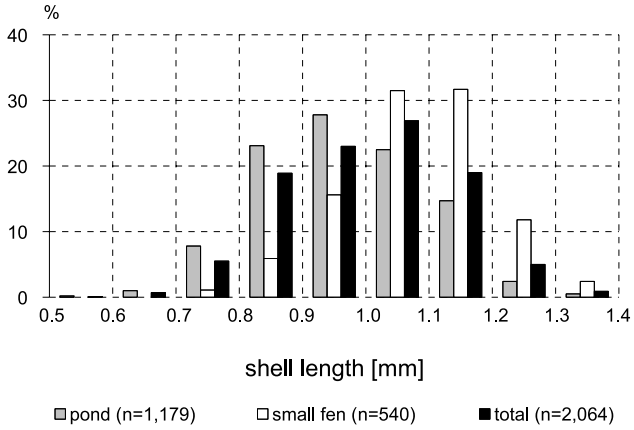


Fig. 24. *Pisidium obtusale*: shell length variation among offspring (total) and 2 examples of variation in populations

Pisidium (*Cyclocalyx*) *obtusale* (Lamarck, 1818)

The species occurred in various kinds of water bodies: lakes, ponds, drainage ditches, and fens (on some wet meadows). In two sites with outflow of water from drains (the small fen on a slope of the Brda valley and concreted ditch at the railway) the shells were thick-walled, with wide poorly protruding umbones, slightly displaced posteriorly and with atypical hinge structure.

Adults with shelled embryos were found from early spring till the end of summer. When placed in the culture, they released offspring from April till October (rarely still in November). According to the literature data (MITROPOLSKIJ 1969, MEIER-BROOK 1970, HEITKAMP 1980) the relatively long period of offspring release results from two consecutive reproductive periods. The number of offspring was correlated with the parent's shell length (r=0.76, n=142) (Fig. 23). In the culture the smallest offspring-releasing (4 young) individual had shell 1.79 mm long. The maximum number of offspring in one reproductive period was 26 (Table 1), and in the other studied populations it did not exceed 20. In one of the populations studied by MEIER-BROOK (1970) the maximum number of offspring was 26.

On release the juveniles had shells 0.51–1.40 mm long (mean 1.01 mm, SD=0.13, n=2.064) (Fig. 24). The mean shell length was: for Lake Sosnowe 0.95 mm, for field pond 0.97 mm, for small fen on the slope of Brda valley 1.09 mm, for concreted ditch 1.11 mm. The height/length ratio was 0.701–0.875 (mean 0.804, SD=0.024, n=1,510) (infra-population differences was rather small). The offspring reached on average 37.6% of the parent's shell length (SD=6.6, n=1,197, range 21.1–58.1%).

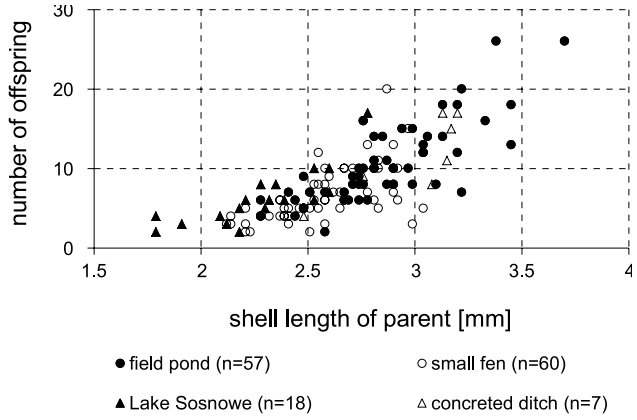


Fig. 23. *Pisidium obtusale*: parent size and number of offspring, divided into studied populations

Pisidium (*Hiberneuglesa*) *hibernicum* Westerlund, 1894

In the studied area the species occurred mainly in the ditches draining lakes Bublinek (1st in the figures) and Sosnowe (2nd in the figures) (less often in lakes). Adults with shelled embryos were found from June till August. When placed in the culture they released offspring from the end of June till September (rarely longer, till October). The number of offspring was correlated with the parent's shell length (r=0.75, n=28) (Fig. 25). The fecundity of large individuals

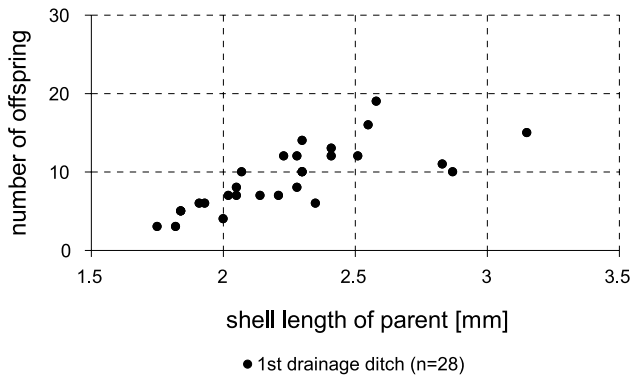


Fig. 25. *Pisidium hibernicum*: parent size and number of offspring

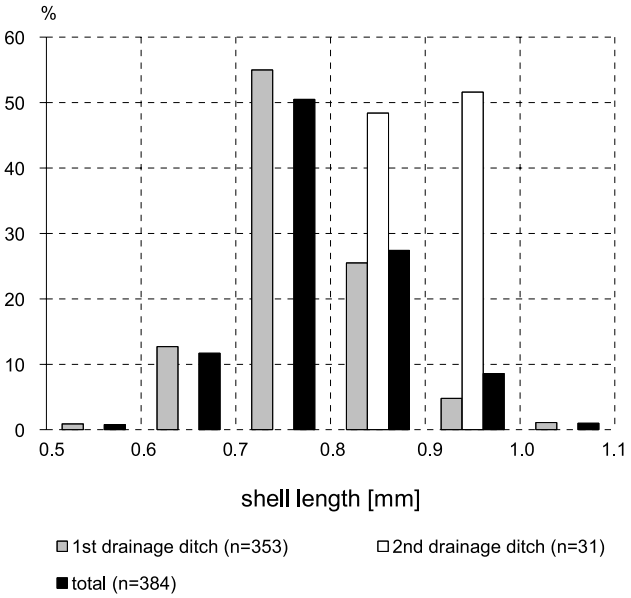


Fig. 26. *Pisidium hibernicum*: shell length variation among offspring (total) and 2 examples of variation in populations

(shell length more than 2.6 mm) decreased gradually. The smallest bivalve in the culture which released offspring (3 young) had shell 1.75 mm long. The maximum number of offspring in one reproductive period was 19 (Table 1). ODHNER (1929) reported from Sweden the maximum of 20 juveniles at shell length of 2.6 mm. The fecundity in the population studied by MEIER-BROOK (1970) was much smaller (not exceeding 8).

On release the juveniles had shells 0.56–1.06 mm long (mean 0.79 mm, SD=0.08, n=384) (Fig. 26) and were slightly smaller than reported by MEIER-BROOK (1970). Mean shell length of offspring was: from ditch draining Lake Bublinek – 0.78 mm, from ditch draining Lake Sosnowe – 0.90 mm. The height/length ratio was 0.768–0.870 (mean 0.831, SD=0.018, n=298) (mean values in the populations 0.833 and 0.817). The offspring reached on average 33.4% of the parent's shell length (SD=4.0, n=261, range 24.6–49.1%). The juvenile shells were distinctly convex and regularly rounded in lateral view (without angles between margins).

Pisidium (*Cingulipisidium*) *milium* Held, 1836

In the studied area the species was found to inhabit various types of water bodies: lakes, some of the oxbows, ponds and drainage ditches. Adults with shelled embryos were found from May to July. In the culture offspring was released mainly in June and July (rarely as early as the end of May, or in August). The number of offspring was closely correlated with the parent's shell length (r=0.87, n=43) (Fig. 27). In the culture the smallest offspring-releasing (3 young) bivalve had shell 1.93 mm long. The maximum number of offspring in one reproductive period was 18 (Table 1), and in another two populations 17 in each. In the populations studied by HEARD (1965) and HOLOPAINEN & JÓNASSON (1989) the number of offspring was smaller, not exceeding 11.

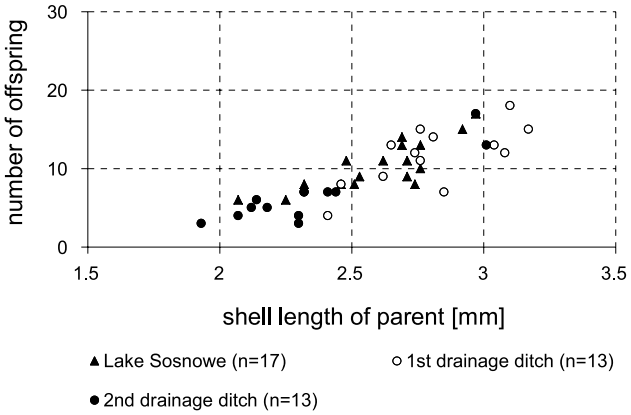


Fig. 27. *Pisidium milium*: parent size and number of offspring, divided into studied populations

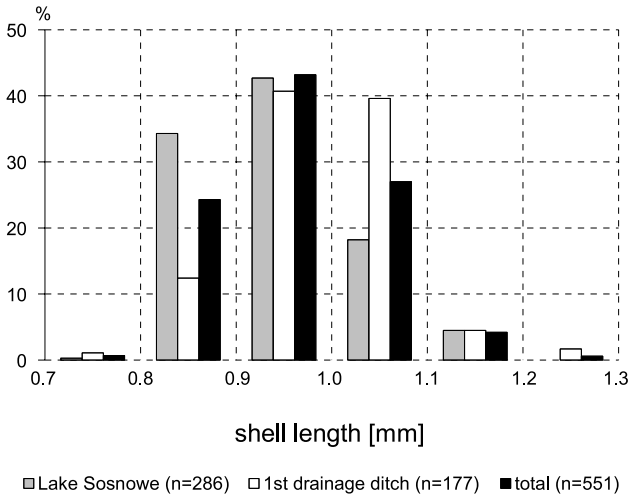


Fig. 28. *Pisidium milium*: shell length variation among offspring (total) and 2 examples of variation in populations

On release the juveniles had shells 0.71–1.22 mm long (mean 0.97 mm, SD=0.08, n=551) (Fig. 28). The mean shell length in the studied populations was 0.95 mm (Lake Sosnowe), 0.97mm (ditch draining Lake Bublinek – 2nd in Fig. 27) and 0.99 mm (ditch draining Lake Sosnowe – 1st in Figs 27–28). The height/length ratio was 0.714–0.829 (mean 0.772, SD=0.021, n=344) (infra-population differences was rather small). The offspring reached on average 36.2% of the parent's shell length (SD=3.9, n=416, range 26.1–48.9%).

Pisidium (*Cingulipisidium*) *pseudosphaerium* Schlesch, 1947

In the studied area the species occurred in water bodies near the village of Korne (Lake Bublinek, its

drainage ditches and in a field pond ca. 250 m west of the lake). Till 2008 the bivalves were fairly numerous in the pond, but probably became extinct after it became inhabited by beaver.

Adults with shelled embryos were found from May to October. When placed in the culture they released offspring from June till the end of October. The number of offspring was correlated with the parent's shell length (r=0.58, n=58) (Fig. 29). In the culture the smallest offspring-releasing (7 young) bivalve had shell 2.30 mm long. The maximum number of offspring in one reproductive period in the pond was 17 (Table 1), and in Lake Bublinek 10.

On release the juveniles had shells 0.76–1.38 mm long (mean 1.05 mm, SD=0.10, n=601) (Fig. 30). The mean shell length in the studied populations was: pond 1.04 mm, Lake Bublinek 1.08 mm. The height/length ratio was 0.711–0.818 (mean 0.763, SD=0.018, n=538). The offspring reached on average 37.2% of the parent's shell length (SD=4.9, n=490, range 28.2–51.9%).

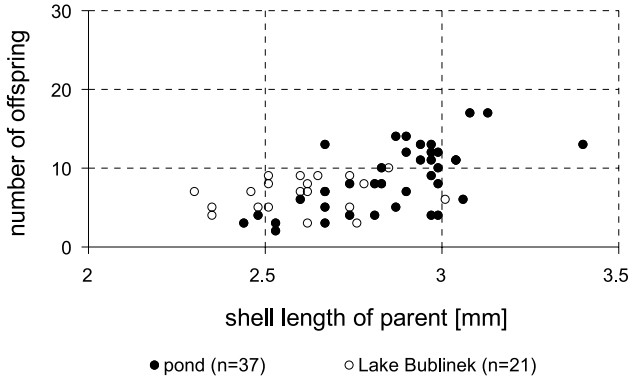


Fig. 29. *Pisidium pseudosphaerium*: parent size and number of offspring, divided into studied populations

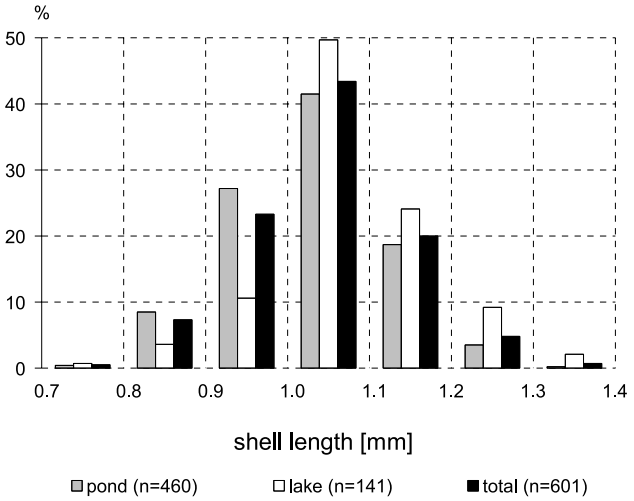


Fig. 30. *Pisidium pseudosphaerium*: shell length variation among offspring (total) and 2 examples of variation in populations

Pisidium (*Cingulipisidium*) *nitidum* Jenyns, 1832

The species occurred in a variety of water bodies: lakes, oxbows, drainage ditches. In the littoral of Lake Sosnowe (sandy bottom, depth 0.1–0.5 m) I found shells corresponding to the description of *P. nitidum* f. *arenicola* Stelfox. They were strongly striated, shiny (like *P. crassum*), but their hinge structure was typical of *P. nitidum*.

Adults with shelled embryos were found mainly from May to July (rarely in April or September). Usually shortly after placing them in laboratory they released offspring. The number of offspring was correlated with the parent's shell length (r=0.74, n=150) (Fig. 31). In the culture the smallest offspring-releasing (2 young) bivalve had shell 1.89 mm long. The maximum number of offspring in one reproductive period was 35 (Table 1), but in the other individuals from that population (Lake Sosnowe) it did not exceed 28. In another population (ditch draining Lake Bublinek) the number was even smaller, not exceeding 24. According to the literature two generations of young appear during the year, usually released from June till September (Odhner 1929, Heard 1965, Ladle & Baron 1969, Meier-Brook 1970, Holopainen & Hanski 1986, Holopainen & Jónasson 1989). The reported maximum numbers of offspring varied from 5 to 26 (Meier-Brook 1970, Holopainen & Hanski 1986).

On release the juveniles had shells 0.55–1.27 mm long (mean 0.91 mm, SD=0.10, n=2,189) (Fig. 32). The mean shell length in Lake Sosnowe was 0.87 mm, in the ditch draining Lake Bublinek 0.96 mm. A similar size of juveniles was reported for example by Ladle & Baron (1969), Meier-Brook (1970), Holopainen & Hanski (1986). The height/length ratio was 0.730–0.840 (mean 0.789, SD=0.016, n=1,243) (infra-population differences were rather small). The offspring

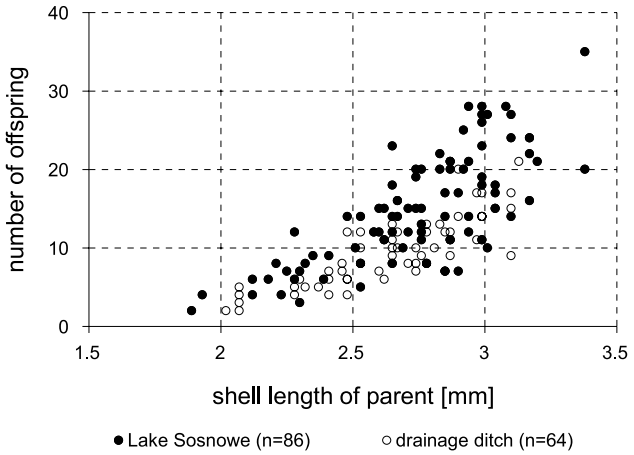


Fig. 31. *Pisidium nitidum*: parent size and number of offspring, divided into studied populations

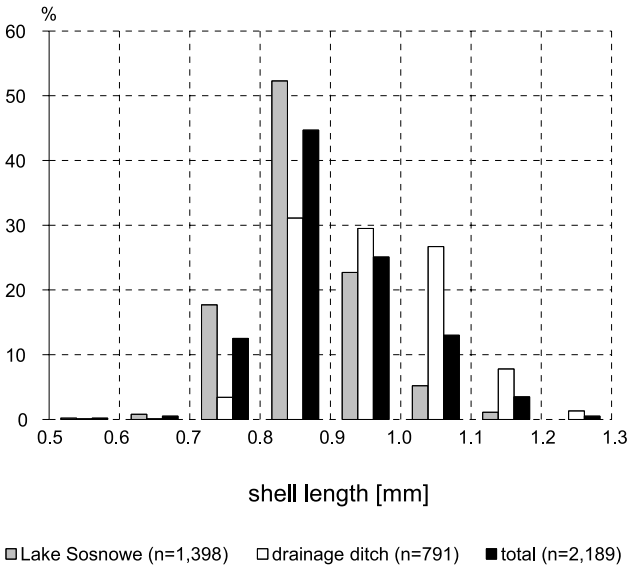


Fig. 32. *Pisidium nitidum*: shell length variation among offspring (total) and 2 examples of variation in populations

reached on average 32.6% of the parent's shell length (SD=5.1, n=1,927, range 17.8–56.1%).

Pisidium (*Cingulipisidium*) *crassum* (Stelfox, 1918)

Bivalves corresponding to STELFOX's (1918) description of *P. nitidum* var. *crassa* occurred on the sandy bottom of Lake Sosnowe (usually at less than 1 m). Some authors regard them as a distinct species *P. crassum* (PIECHOCKI 1991, PIECHOCKI & DYDUCH-FALNIOWSKA 1993, GLÖER & ZETTLER 2005, PIECHOCKI & SULIKOWSKA-DROZD 2008, GLÖER & DIERCKING 2010, PIECHOCKI & WAWRZYNIAK-WYDROWSKA 2016), others as a form of the rather variable *P. nitidum*. In the studied site they differed from *P. nitidum* f. *arenicola* in their relatively wide and strongly bent hinge plate, with massive lateral teeth and a different shape of cardinal teeth.

Adults collected in spring released offspring from April to June, those collected in autumn and winter reproduced from December to February. The number of offspring was closely correlated with the parent's shell length (r=0.89, n=19) (Fig. 33). In the culture the smallest offspring-releasing (2 young) bivalve had shell 2.02 mm long. The maximum number of offspring in one reproductive period was 30 (Table 1).

On release the juveniles had shells 0.56–0.95 mm long (mean 0.74 mm, SD=0.07, n=735) (Fig. 34). The height/length ratio was 0.722–0.852 (mean 0.795, SD=0.023, n=604). The offspring reached on average 29.5% of the parent's shell length (SD=3.1, n=293, range 17.9–36.6%).

The newborn *P. crassum* were usually smaller than *P. nitidum* (Fig. 35), but their proportions were sim-

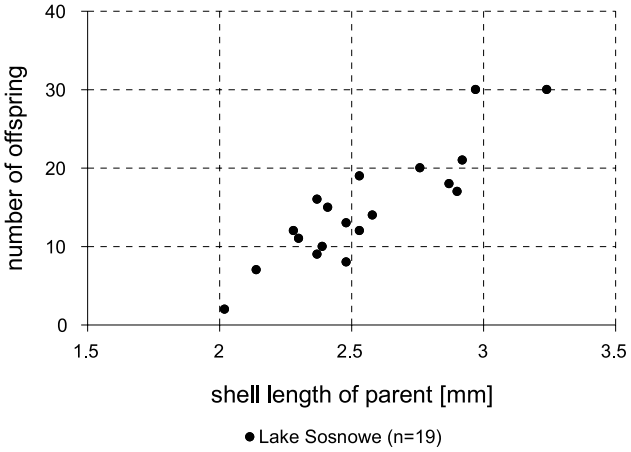


Fig. 33. *Pisidium crassum*: parent size and number of offspring

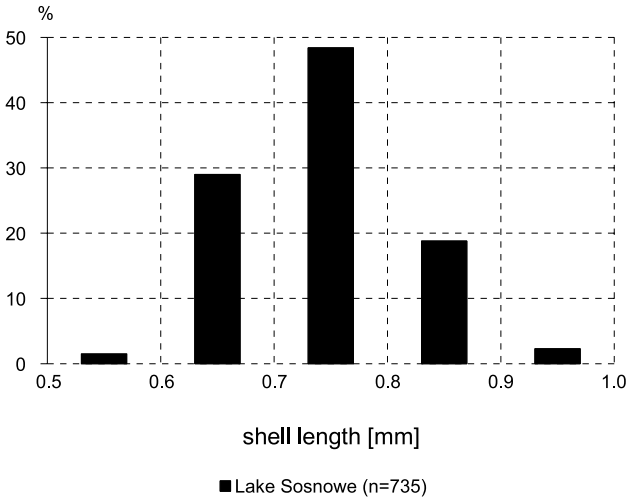


Fig. 34. *Pisidium crassum*: shell length variation among offspring

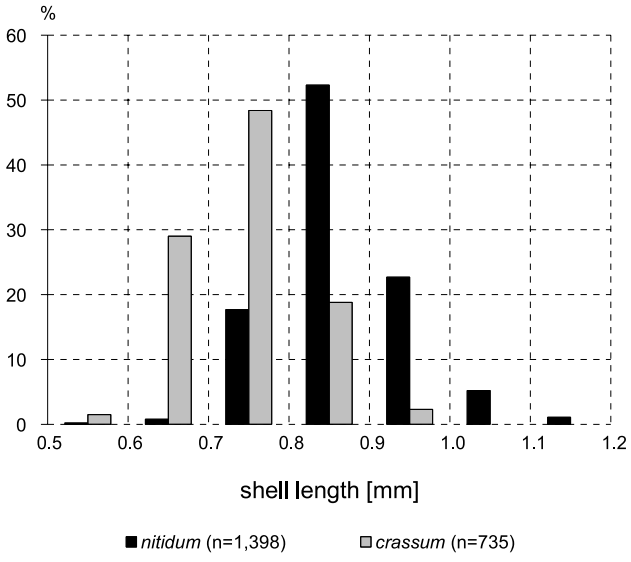


Fig. 35. Comparison of *Pisidium crassum* and *P. nitidum*: shell length variation among offspring

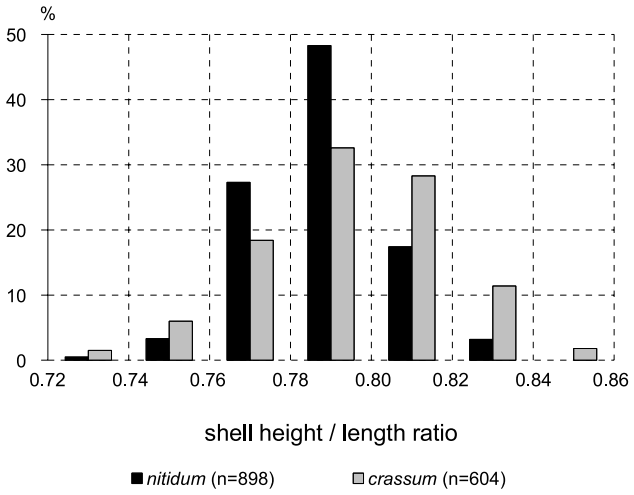


Fig. 36. Comparison of *Pisidium crassum* and *P. nitidum*: variation in shell proportions among offspring

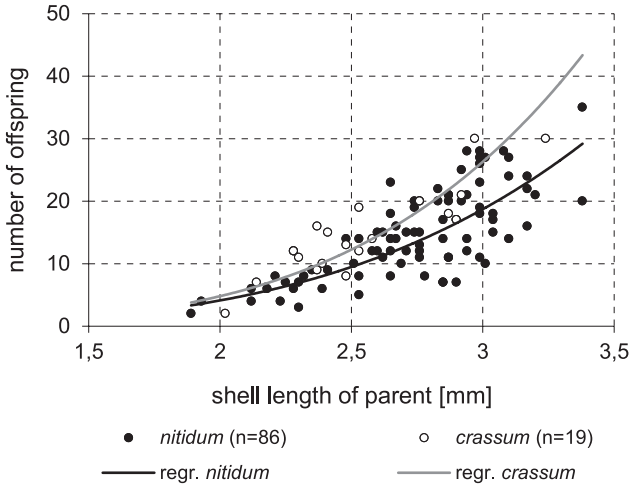


Fig. 37. Comparison of *Pisidium crassum* and *P. nitidum*: parent size and number of offspring

ilar (Fig. 36). At the same parent's shell length the mean number of offspring in *P. crassum* was greater than in *P. nitidum* (Fig. 37).

Pisidium (*Pseudeupera*) *subtruncatum* Malm, 1855

In the study area the species was rather common and occurred in various kinds of water bodies: lakes, rivers, oxbows, drainage ditches, fish ponds. Adults collected in April–June released offspring from May till the beginning of July, and those collected later (July–September) reproduced soon after they were placed in the culture. The periods of offspring release reported in the literature vary (LADLE & BARON 1969, DYDUCH-FALNIOWSKA 1983, HOLOPAINEN & JÓNASSON 1983, MOUTHON 2005, PIECHOCKI & WAWRZYNIAK-WYDROWSKA 2016). The number of offspring was closely correlated with the parent's shell length (r=0.82, n=99) (Fig. 38). In the culture

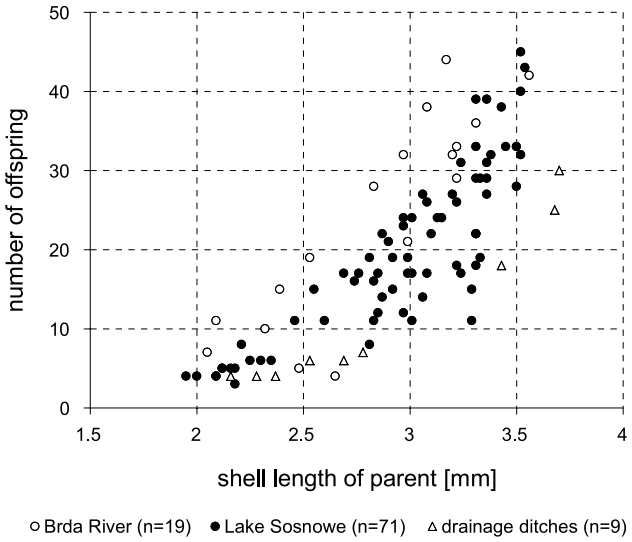


Fig. 38. *Pisidium subtruncatum*: parent size and number of offspring, divided into studied populations

the smallest offspring-releasing (4 young) individual had shell 1.95 mm long. The maximum number of offspring in one reproductive period was: for Lake Sosnowe 45 (Table 1), for Brda River 44, in the remaining populations it did not exceed 30. According to the literature the bivalves started reproduction at shell length of 1.7–2.2 mm and released at most 12–25 juveniles (LADLE & BARON 1969, HOLOPAINEN & JÓNASSON 1983). According to MOUTHON (2005) the number of young depended on the population density.

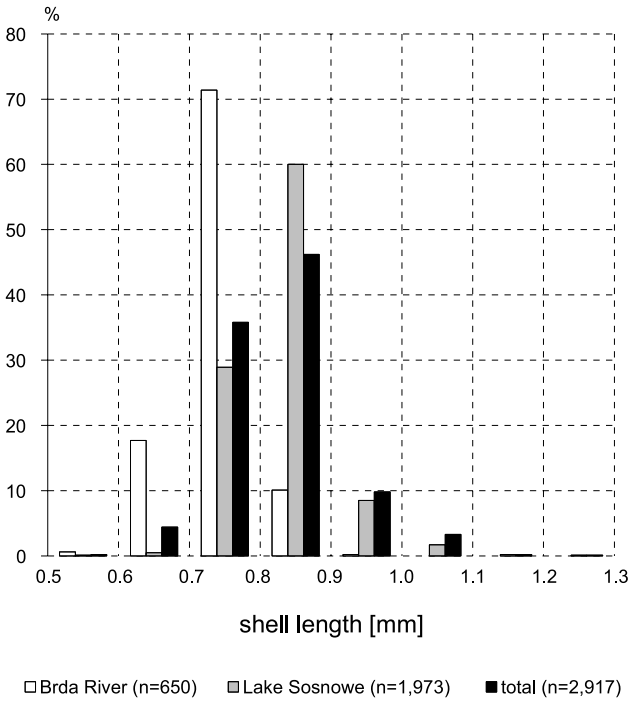


Fig. 39. *Pisidium subtruncatum*: shell length variation among offspring (total) and 2 examples of variation in populations

On release the juveniles had shells 0.53–1.27 mm long (mean 0.83 mm, SD=0.08, n=2,917) (Fig. 39). In the studied populations the shell length varied from 0.74 (Brda) to 1.00 mm (ditch draining Lake Sosnowe). The height/length ratio was mostly 0.82–0.84 (mean 0.833, SD=0.016, n=2,095, range 0.781–0.879) (infra-population differences were rather small). The offspring reached on average 26.8% of the parent's shell length (SD=4.4, n=1,943, range 16.4–51.7%). The juvenile shells were close to trapezoidal with rounded angles, and the anterior, dorsal and posterior margins were of similar length.

The bivalves from the Brda, under the bridge (road from Sąpolno to Czosnowo) corresponded to the description of *P. subtruncatum* var. *tenuilineatiformis* Feliksiak (shells with distinct, dense striation). One of them, found on 20.04.1999 (shell length 1.98 mm) released 6 young after 10 days. The juvenile shells were 0.63–0.66 mm long and did not differ from the typical *P. subtruncatum*.

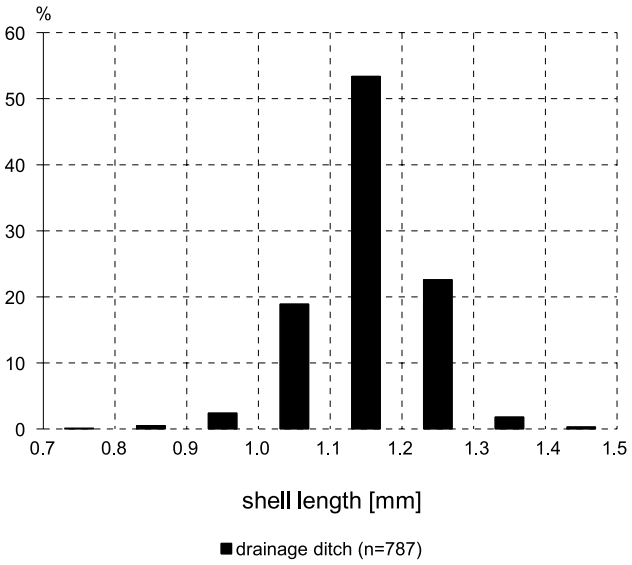


Fig. 41. *Pisidium pulchellum*: shell length variation among offspring

Pisidium (*Pseudeupera*) *pulchellum* Jenyns, 1832

In the studied area the species occurred in a short section (ca. 30 m) of the ditch draining Lake Sosnowe. In 2008 the locality was destroyed by beaver. Adults with shelled embryos were found mainly in May and June. When placed in the culture they released offspring in June and July. Single adults with shelled embryos were still found at the end of August (offspring release in August or September). The number of offspring was closely correlated with the parent's shell length (r=0.91, n=22) (Fig. 40). In the culture the smallest offspring-releasing (3 young) bivalve had shell 2.65 mm long. The maximum number of offspring in one reproductive period was 22 (Table 1).

On release, the juveniles had shells 0.78–1.50 mm long (mean 1.16 mm, SD=0.08, n=787) (Fig. 41). The height/length ratio was 0.750–0.839 (mean 0.793, SD=0.017, n=723). The umbonal part of the shell was smooth, and a few wide striae were usually visible near the ventral margin. The offspring reached on average 32.7% of the parent's shell length (SD=2.8, n=315, range 25.5–46.7%).

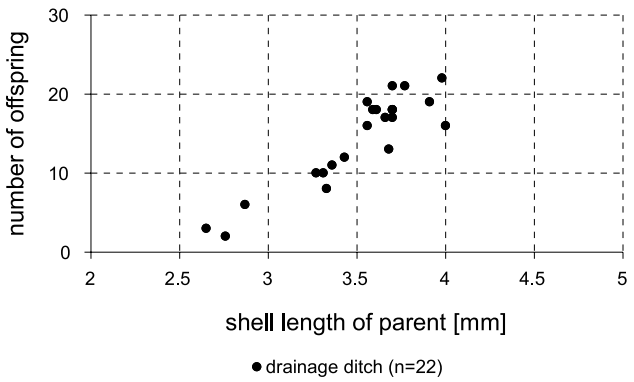


Fig. 40. *Pisidium pulchellum*: parent size and number of offspring

Pisidium (*Henslowiana*) *henslowanum* (Sheppard, 1823)

The species occurred in lakes, rives, oxbows converted to fish ponds and in the ditches draining the ponds. Adults with shelled embryos were usually found from half of April till half of June. When placed in the culture they released offspring from May to July. The number of offspring varied, with the max-

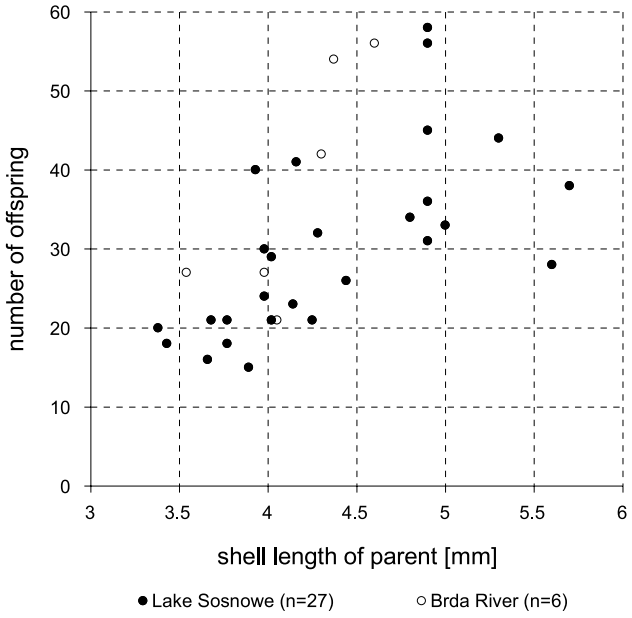


Fig. 42. *Pisidium henslowanum*: parent size and number of offspring, divided into studied populations

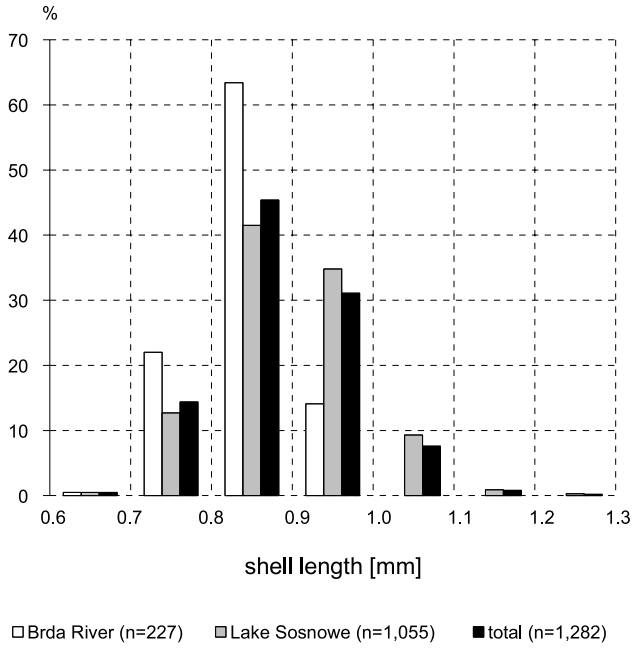


Fig. 43. *Pisidium henslowanum*: shell length variation among offspring (total) and 2 examples of variation in populations

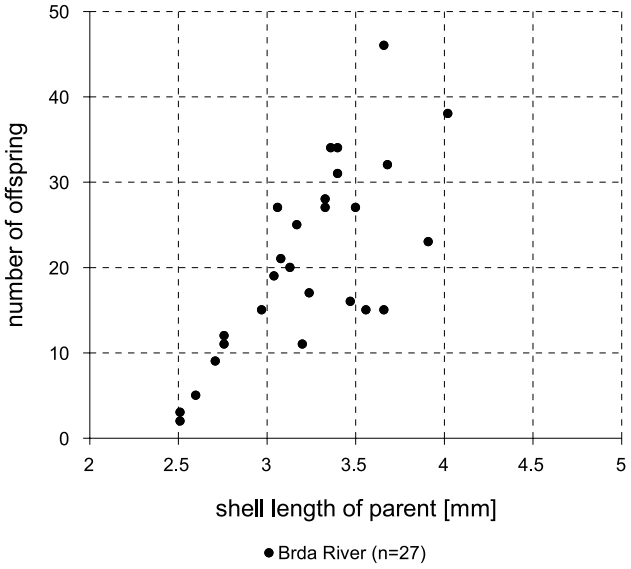


Fig. 44. *Pisidium supinum*: parent size and number of offspring

imum at parent's shell length of 4.6–4.9 mm, and then decreased (Fig. 42). The correlation between the parent's shell length and the number of offspring was r=0.58, n=33. In the culture the smallest offspring-releasing (20 young) bivalve had shell 3.38 mm long (no smaller individuals could be collected). The maximum number of offspring in one reproductive period was: for Lake Sosnowe – 58 (Table 1), for Brda River – 56. According to the literature data the species has one or two reproductive periods in a year (HOLOPAINEN 1979, HOLOPAINEN & JÓNASSON 1989, PETTINELLI & BICCHIERAI 2009). In the populations studied by MITROPOLSKIJ (1970) and HOLOPAINEN (1979) the maximum number of offspring was 40.

On release, the juveniles had shells 0.64–1.24 mm long (mean 0.89 mm, SD=0.08, n=1,282) (Fig. 43). The mean shell length in the Brda was 0.85 mm, in Lake Sosnowe 0.90 mm. The height/length ratio was 0.674–0.813 (mean 0.753, SD=0.028, n=234). On large shells there was a well-developed fold roughly at half height, on small shells it was close to the lower margin (arcuately bent in the way opposite to the shell margin). The offspring reached on average 20.2% of the parent's shell length (SD=2.4, n=1,062, range 14.0–29.8 %). The newly released young were very active.

Pisidium (*Henslowiana*) *supinum* A. Schmidt, 1851

In the studied area the species occurred in the rivers Brda and Lipczynka. Adults collected from the end of April till the beginning of June released offspring from May to August, those collected later (e.g. half of August) released their offspring just after being placed in the culture. Those collected too early (around half of April) often started releasing young only as late as 3–4 months after being placed in the culture, and the number of offspring was rather small (omitted in Fig. 44). The number of offspring was correlated with the parent's shell length (r=0.74, n=27) (Fig. 44). In the culture the smallest offspring-releasing (3 young) individual had shell 2.51 mm long. The maximum number of offspring in one reproductive period was 46 (Table 1) and was close to that reported by MOUTHON (2011). That author observed offspring release in France in two periods: May–June and August, and the smallest adults with shelled embryos had shells 1.68 mm long.

On release, the juveniles had shells 0.52–1.29 mm long (mean 0.80 mm, SD=0.10, n=658) (Fig. 45). The height/length ratio was 0.734–0.833 (mean

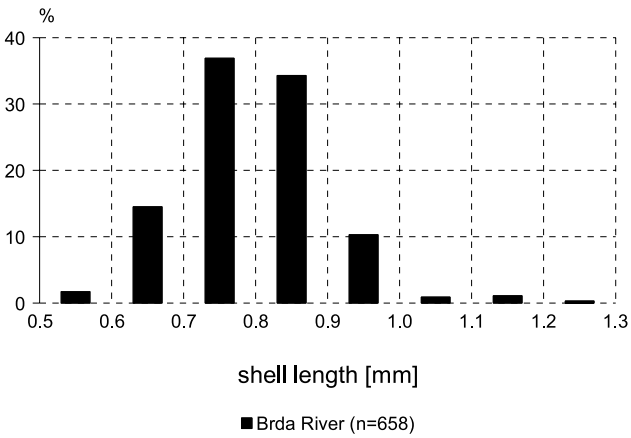


Fig. 45. *Pisidium supinum*: shell length variation among offspring

0.781, SD=0.021, n=219). The fold (usually much smaller than in *P. henslowanum*) on medium-sized shells was located roughly at half height. The offspring reached on average 23.6% of the parent's shell length (SD=3.2, n=635, range 17.0–39.4%). The newly released young were very active.

Pisidium (*Odhneripisidium*) *moitessierianum* Paladilhe, 1866

In the studied area the species occurred in the Brda River. Adults with shelled embryos were found mainly in April and May (rarely as early as in March), and offspring was released shortly after placing the bivalves in the culture. Also at the end of summer some individuals reproduced; they released offspring in September and October. The number of offspring varied and was rather poorly correlated with the parent's shell length (r=0.57, n=53) (Fig. 46). In the culture the smallest offspring-releasing (7 young) individual had shell 1.50 mm long. The maximum number of offspring released in one reproductive period was 21 (Table 1). In Finland the species had one reproductive period in a year and released offspring in July (HOLOPAINEN 1979). In France offspring was released in two periods: May–June and August–September (MOUTHON 2011). In France the maximum number of offspring in one reproductive period was 17 (MOUTHON 2011), according to other authors it was much smaller (HOLOPAINEN 1979, GRIGOROVICH et al. 2000).

On release, the juveniles had shells 0.46–0.80 mm long (mean 0.59 mm, SD=0.05, n=724) (Fig. 47). The height/length ratio was 0.707–0.816 (mean 0.758, SD=0.019, n=432). The roll-like thickening visible around the umbonal part of adult shells was usually located at the margin of the newborns' shells. The offspring reached on average 33.9% of the parent's shell length (SD=3.7, n=550, range 26.1–45.9%). The juvenile measurements reported in the literature were within the above variation range (HOLOPAINEN 1979, HOLOPAINEN & HANSKI 1986, MOUTHON 2011).

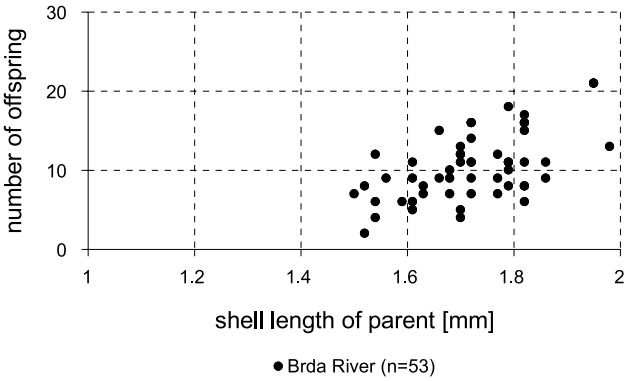


Fig. 46. *Pisidium moitessierianum*: parent size and number of offspring

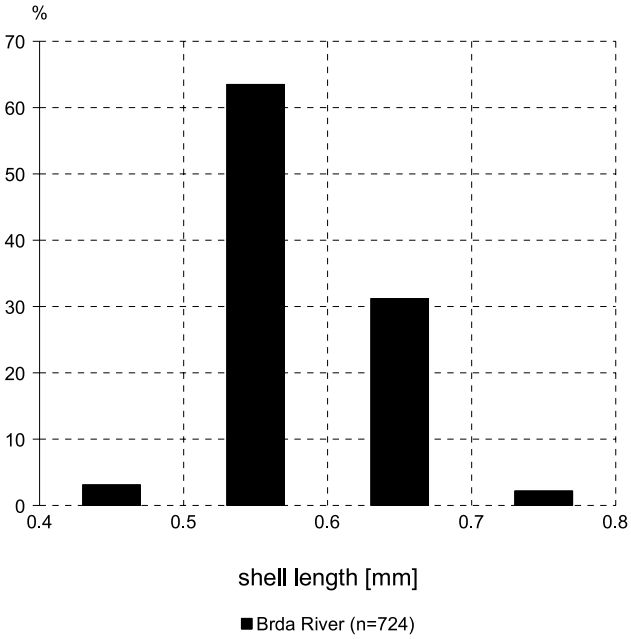


Fig. 47. *Pisidium moitessierianum*: shell length variation among offspring

COMPARATIVE REMARKS

The occurrence of as many as 16 species of *Pisidium* offered a unique opportunity to compare their reproductive parameters without the need to consider the effect of climate conditions. The variation in the shell length of juveniles and the shell proportions is presented in Figures 48 and 49. Figure 50 presents the variation of relative size of the offspring (ratio of juvenile to parent shell length). Species of the same subgenus were placed next to each other (as in the text). Particular reproductive parameters differed more or less distinctly not only between the species, but also between conspecific populations from different habitats. The anatomical structure (division into subgenera) had no greater effect on the differences in the studied parameters.

The number of offspring was positively correlated with the parent's shell length, and the regression curves were best described by exponential equations (different between species and even populations). For *P. pulchellum* the exponent was the highest and amounted to 5.3, for *P. supinum* 4.6, for *P. crassum* 4.2, and for *P. nitidum* and *P. ponderosum* 4.0 (it was smaller for the remaining species). This resulted from the fact that the mean fecundity of the pisids depended mainly

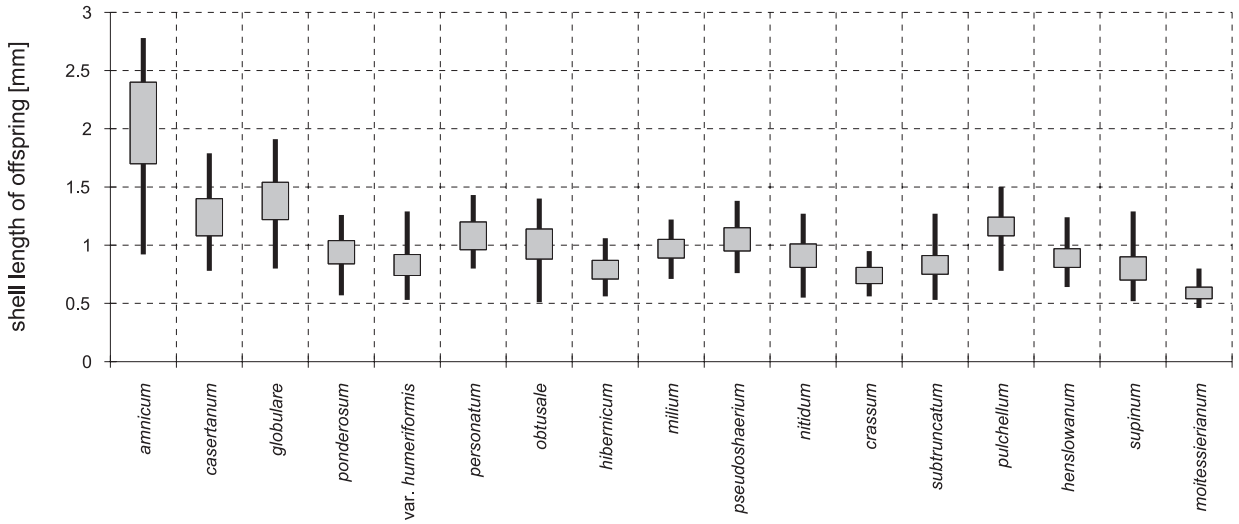


Fig. 48. Genus *Pisidium*: comparison of shell length of offspring; black lines – ranges, bars – mean ± SD

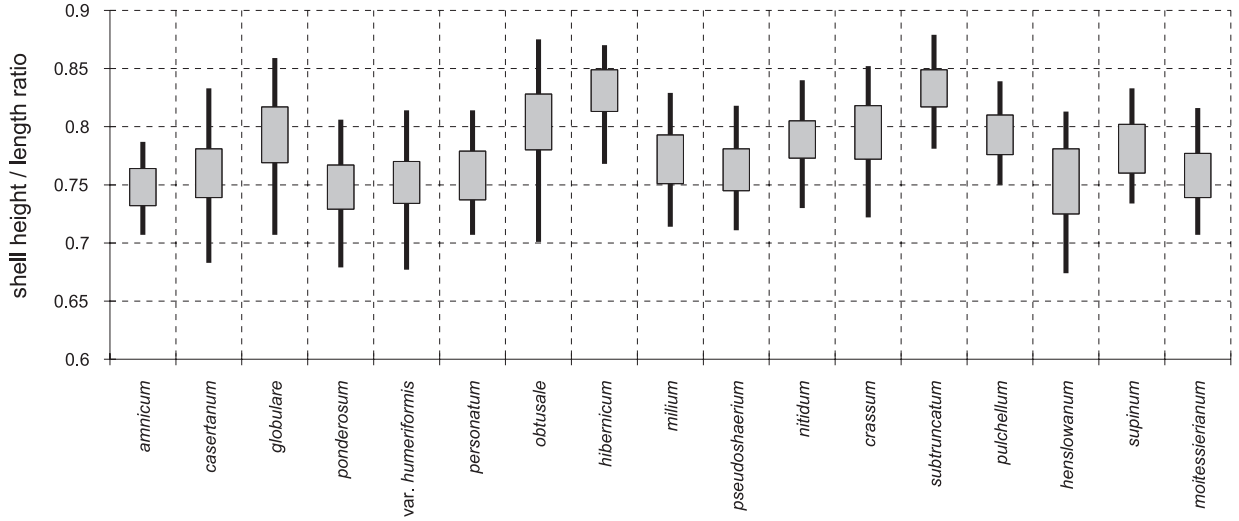


Fig. 49. Genus *Pisidium*: comparison of shell proportions (height/length ratio) of offspring; black lines – ranges, bars – mean ± SD

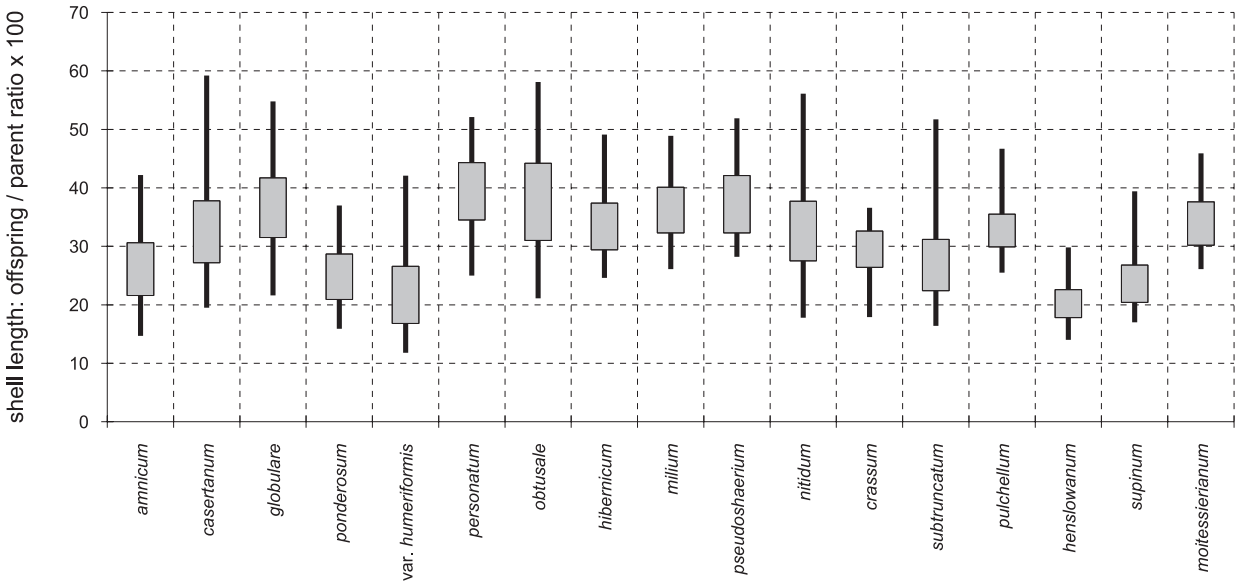


Fig. 50. Genus *Pisidium*: comparison of relative size of offspring; black lines – ranges, bars – mean ± SD

on their size. However, also other factors (e. g. mortality of embryos) had an effect on the parent's actual fecundity. Too great a number of released offspring in relation to the parent size resulted in a small size of the released young (limited space for incubation). When most individuals in a population were very fecund, the mean size of the offspring decreased (and vice versa).

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