

THE FECUNDITY, TIME OF EGG DEVELOPMENT AND JUVENILE PRODUCTION IN SPINY-CHEEK CRAYFISH (*ORCONECTES LIMOSUS*) UNDER CONTROLLED CONDITIONS

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ABSTRACT

We comprehensively describe the fecundity and time of embryonic development of the spiny-cheek crayfish (*Orconectes limosus*). Linear relationships between female size and ovarian fecundity, pleopodal fecundity, and production of juveniles at the 3rd stage, were confirmed. The ovarian fecundity was evaluated for the smallest as well as largest females in the sampled population (43-93 mm of body length); the number of oocytes (eggs) ranged widely, between 46 and 505. No significant difference was found between the ovarian and pleopodal fecundity observed just after egg laying. The value of the female gonadosomatic index just before laying was $4.2 \pm 1.8\%$ (0.8-7.7%). The mean diameter of eggs on female pleopods was 1.8 ± 0.2 mm (1.45-2.15 mm). A statistically significant difference was found between the numbers of eggs carried on individual pairs of pleopods. Mean time from laying to hatching was 46 ± 3.8 days (37-56 days), i.e. 647 ± 39.9 CTU (Celsius Temperature Units = degrees Celsius \times days). Mean production of juveniles at the 3rd stage was found to be 135.7 ± 67.24 (15-243) juveniles. The early sexual maturation and also high number of juveniles at the 3rd stage per female gives this species a good predisposition for quick establishment in new localities.

Key-words: Crayfish, *Orconectes limosus*, lifecycle, Czech Republic, juveniles, egg development.

LA FÉCONDITÉ, LA DURÉE DU DÉVELOPPEMENT EMBRYONNAIRE ET LA PRODUCTION DE JUVÉNILES CHEZ L'ÉCREVISSE AMÉRICAINE (*ORCONECTES LIMOSUS*) DANS UN ENVIRONNEMENT CONTRÔLÉ

RÉSUMÉ

Cette étude décrit en détail la fécondité et la durée de développement embryonnaire de l'écrevisse américaine (*Orconectes limosus*) et confirme le rapport direct entre la taille de la femelle, la fécondité ovarienne, pléopodale et la production de juvéniles au stade 3. La fécondité ovarienne a été évaluée pour les femelles les plus petites aussi bien que pour les plus grandes femelles de la population échantillonnée (longueur corporelle de 43 à 93 mm). Le nombre d'oocytes varie fortement, entre 46 et 505. On n'a pas trouvé de différence

significative entre la fécondité ovarienne et la fécondité pléopodale, observées juste après la ponte. La valeur de l'indice gonadosomatique (I.G.S.) trouvée juste avant la ponte est de $4,2 \pm 1,8$ % (0,8-7,7 %) pour les femelles et de $0,3 \pm 0,05$ % (0,2-0,4 %) pour les mâles. Le diamètre moyen des œufs sur les pléopodes des femelles était de $1,8 \pm 0,2$ mm (1,45-2,15 mm). Le nombre d'œufs sur les paires individuelles de pléopodes était très variable (95 à 492). La durée moyenne entre la ponte et l'éclosion était de $46 \pm 3,8$ jours (37 à 56 jours), i.e. $647 \pm 39,9^\circ$ Celsius \times jour (543 à 730). La production moyenne de juvéniles au stade 3 fut de $135,7 \pm 67,24$ (15 à 243) juvéniles. La maturité sexuelle plus précoce et le grand nombre de juvéniles de stade 3 produits par femelles donnent à cette espèce une prédisposition à occuper plus rapidement de nouveaux sites.

Mots-clés : Écrevisse, *Orconectes limosus*, cycle biologique, République tchèque, juvéniles, développement des œufs.

INTRODUCTION

The spiny-cheek crayfish (*Orconectes limosus*) (Rafinesque) is originally native to the east coast of the USA and Canada (HOBBS, 1974; HAMR, 2002). This species was imported to Europe in 1891. Nowadays, it is widely distributed throughout most Western- and Central European countries (HOLDICH *et al.*, 1999). It is one of five crayfish species that are currently present in open waters of the Czech Republic. The noble crayfish *Astacus astacus* (Linnaeus), stone crayfish *Austropotamobius torrentium* (Schrank), narrow-clawed crayfish *Astacus leptodactylus* (Eschscholtz) and signal crayfish *Pacifastacus leniusculus* (Dana) are also present.

Although the first report of the presence of the spiny-cheek crayfish on the Czech territory was published at the end of the 1980's, the species seems to have been present in the river Elbe already in the 1960's. By the end of 20th century, it had spread widely in the Elbe watershed, due to its natural dispersal potential as well as a result of anthropogenic translocations (KOZÁK *et al.*, 2004; PETRUSEK *et al.*, 2006). This species is a major vector of the crayfish plague pathogen, *Aphanomyces astaci*, in Czech open waters (KOZUBÍKOVÁ *et al.*, 2006).

The spiny-cheek crayfish shows several characteristics such as rapid maturation, short-lifespan, high fecundity and second mating period, which facilitate its fast population growth, dispersal and invasive capabilities. In Québec populations, mating takes place in September-October and again in March-April (HAMR, 2002). According to BRINK *et al.* (1988), the mating period for *O. limosus* occurs in autumn, just as it does for *A. astacus*, *A. leptodactylus* and *P. leniusculus*. HAMR (2002) states, however, that in American and European populations mating also takes place in spring, and eggs are carried from March to May. BRINK *et al.* (1988) captured ovigerous females of *O. limosus* from mid-March to May. A similar period for egg development has been presented by PIELOW (1938), SMITH (1981) and ORZECZOWSKI (1984). SMITH (1981) and BRINK *et al.* (1988) observed that larger and presumably older females of *O. limosus* extruded their eggs earlier in the season than smaller and younger ones. A temporal difference in the onset of the breeding period between younger and older females is probably a more common phenomenon in orconectid crayfish, as it is also known for *Orconectes immunis* (TACK, 1941).

The potential reproductive capacity of crayfish is usually measured by ovarian egg counts, and realised reproductive capacity by pleopod egg counts. Pleopod egg counts are typically more variable and lower in total numbers than ovarian counts because of incomplete egg extrusion at spawning, eggs that fail to be fertilised, eggs that fail to attach after extrusion or because of losses of attached eggs during the incubation period for various reasons (MASON, 1977; SAVOLAINEN *et al.*, 1996). Pleopod egg counts are more informative when determining recruitment to a population and are therefore more

useful when management of a population is involved (LEWIS, 2002). In *Austropotamobius pallipes*, the ovarian fecundity differs from pleopodal egg counts by 20-40% (REYNOLDS, 2002). In White Lake (Ireland), the observed shortfall in *Austropotamobius pallipes* pleopodal egg number relative to ovarian fecundity was about 30%, but females immediately after spawning had retained at most 2% of their eggs in ovaries or oviducts. This suggests that the discrepancy between the two measures of fecundity is chiefly due to poor egg attachment, rather than to factors such as egg resorption or incomplete fertilisation (SAVOLAINEN *et al.*, 1996; REYNOLDS, 2002). Both ovarian and pleopodal fecundity correlated with female size (STYPIŃSKA, 1973; SAVOLAINEN *et al.*, 1996; AUSTIN, 1998a; SCHULZ and ŠMIETANA, 2001; HARLIOĞLU *et al.*, 2004; MAZLUM and EVERSOLE, 2004; NAKATA and GOSHIMA, 2004; HUBER and SCHUBART, 2005; MAGUIRE *et al.*, 2005), but the relationship between the egg number and body size was strongly influenced by environmental conditions (REYNOLDS, 2002). Different authors evaluated the pleopodal fecundity just after ovulation (ABRAHAMSSON, 1971; AUSTIN, 1998a,b; LEONARD *et al.*, 2001; NAKATA and GOSHIMA, 2004; CELADA *et al.*, 2005a; SÁEZ-ROYUELA, 2005), during incubation (JONES, 1995; LEWIS and HORTON, 1997; MAZLUM and EVERSOLE, 2004; CELADA *et al.*, 2005a,b; SÁEZ-ROYUELA, 2005) or just before hatching (SÖDERBÄCK, 1995; SAVOLAINEN *et al.*, 1996; CELADA *et al.*, 2005b; SÁEZ-ROYUELA *et al.*, 2005).

STYPIŃSKA (1973) recorded an average ovarian fecundity of spiny-cheek crayfish from 315 to 440 eggs related to size group (body length of females ranged from 75 to 104 mm). KOZÁK and POLICAR (in press) found a mean ovarian fecundity (females from 52-82 mm of body length) of 140 eggs, with a minimum of 76 and maximum of 290 eggs.

PIELOW (1938) observed pleopodal fecundity of 241-394 eggs in the spiny-cheek crayfish females (body length ranging from 66 to 92 mm) just two days after laying. Three weeks after the laying, however, the average pleopodal fecundity values were lower – 130 eggs with a minimum and maximum of 2 and 316 eggs, respectively. HOLDICH and LOWERY (1988) presented a pleopodal fecundity of 400 eggs for a spiny-cheek crayfish female with a carapace length of 45 mm. MOMOT in HOLDICH and LOWERY (1988), however, presented a much lower value of mean pleopodal fecundity – 163 eggs. STUCKI (2002) found a mean average pleopodal fecundity of 139 eggs with minimum and maximum 31 and 555 eggs, respectively. HAMR (2002) collected data of several authors and presented pleopodal fecundity ranging between 57 and 440 eggs.

The aim of our study was to comprehensively describe the fecundity and the time of embryonic development of the spiny-cheek crayfish under Central European conditions.

MATERIAL AND METHODS

Crayfish used in the experiment were collected on April 18 and April 26, 2004 in the Kořensko reservoir (Vltava River, South Bohemia, Czech Republic). We measured the body length, carapace length and weight of all crayfish.

Ovarian and pleopodal fecundity

Ovarian fecundity of 20 females was evaluated on April 18, just after catching. We selected individuals that represented both the smallest and largest size fractions of mature females in the sample. Total whole body wet weight of each individual was determined to the nearest 0.1 g on an electronic balance. Each crayfish was then dissected and its gonad was removed. The gonad was weighed on an electronic balance to the nearest 0.0001 g. The gonadosomatic index (GSI; ratio of wet weight of ovary to the whole body

wet weight $\times 100$) was calculated for each crayfish. The number of eggs in the ovaries was counted.

The laying of eggs took place at the end of April and beginning of May. Altogether, 16 females were kept in a special apparatus with shelters in a flow-through system throughout this period. Pleopodal fecundity was evaluated approximately 3 days after the laying. Eggs were removed and counted individually from each pleopod.

Number of juveniles at the 3rd stage

Altogether, 20 females without eggs were stocked individually on April 18 in the Rückel-Vacek hatching apparatus (originally used for hatching salmonid eggs) with a flow-through system. We observed the time of egg laying, hatching and the time of juvenile independence (3rd stage); observations were done only twice a week to minimize disturbance and manipulation. Just after reaching the 3rd stage, we counted the number of juveniles.

Time of embryonic development

Altogether, 80 females were kept in 4 special apparatuses (4 \times 20 females) with shelters in a flow-through system. Females were individually marked with a gloss-paint pen by writing their individual number on the carapace (see SINT and FÜREDER, 2004). Females were checked daily to observe time of laying and subsequently time of juvenile hatching. This allowed us to record the specific time of laying and hatching, but unfortunately caused daily disturbance of females.

Water temperature and outside air temperature were measured automatically by temperature sensors RT-F52 (Qi Analytical Ltd. CZ) at one hour intervals during all experiments (Figure 1). The CTU (Celsius Temperature Units = degrees Celsius \times days) was calculated.

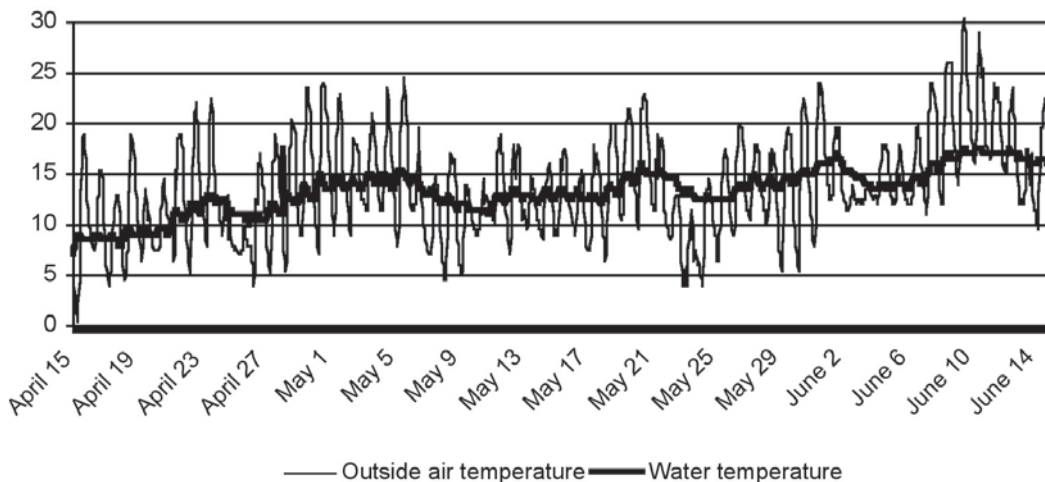


Figure 1

The course of water temperature and outside air temperature during experiments, measured every hour.

Figure 1

Température de l'eau et de l'air extérieur au cours des expériences, mesurées toutes les heures.

Data analysis

Average values of the acquired parameters and SD were counted. Statistical significance was assessed using one-way analysis of variance (ANOVA, Statgraphics version 5), followed by Tukey HSD multiple range test comparisons. The difference between ovarian and pleopodal fecundity was tested by ANCOVA, using the female body length as a covariate. Linear regression was evaluated from the following parameters: ovarian and pleopodal fecundity, and number of juveniles at the 3rd stage, and assessed with Statgraphics version 5. Probability values < 0.01 were considered to be significant.

Results

Ovarian fecundity

The body length and weight of 20 mature females used in the experiment was 54.1 ± 12.64 mm (43-93 mm) and 5.08 ± 5.16 g (2.24-23.37 g), respectively.

The mean ovarian fecundity was found to be 130.8 ± 107.6 , ranging from 46 to 505 eggs. The ovarian fecundity showed a linear relationship ($r^2 = 0.9042$, $P < 0.0000$) to the body length (Figure 2). The average size of eggs was found to be 1.2 ± 0.2 mm (0.9-1.7 mm). We did not find any significant relationship between the size of eggs and their number. Respective to the size of females, however, the largest females had a higher number of the biggest eggs (1.6-1.7 mm), and had also the highest values of GSI (6.45-7.74%). The average gonadosomatic index of females was found to be $4.2 \pm 1.8\%$ (0.83-7.74%).

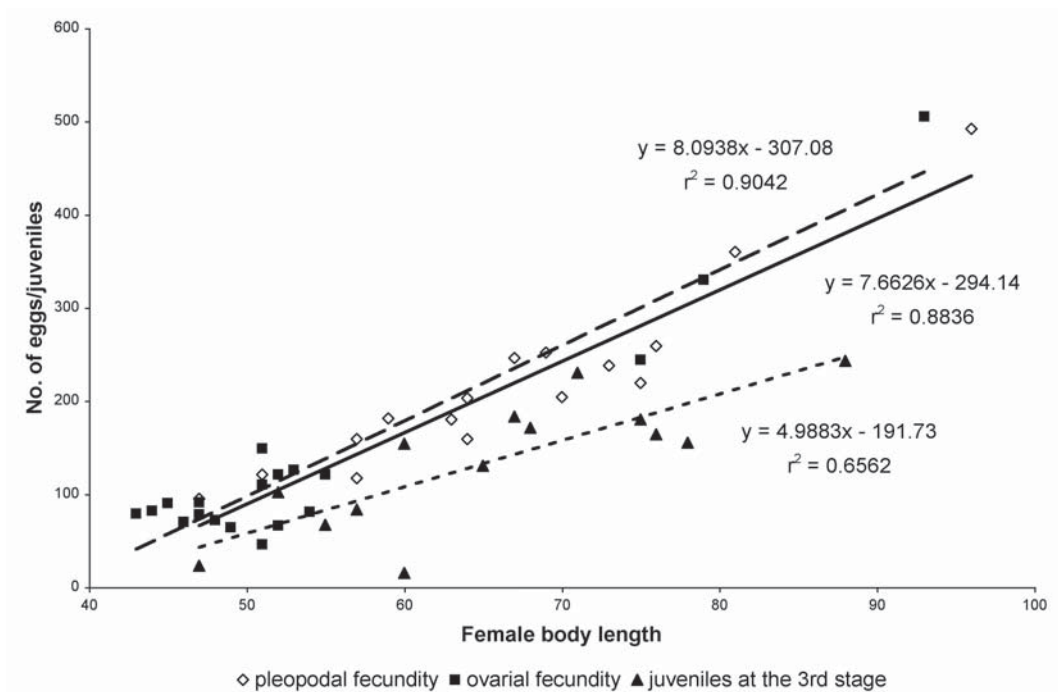


Figure 2

The relationship between the body length and ovarian fecundity, pleopodal fecundity, and production of juveniles at the 3rd stage in spiny-cheek crayfish females (*Orconectes limosus*).

Figure 2

Relation entre la fécondité ovarienne et pléopodale et la production de juvéniles au stade 3, chez l'écrevisse américaine (*Orconectes limosus*).

Pleopodal fecundity

The body length and weight of 16 females used in the experiment was 66.8 ± 11.68 mm (47-96 mm) and 10.86 ± 6.86 g (3.10-29.91 g), respectively. The mean pleopodal fecundity was found to be 217.8 ± 94.9 (95-492) eggs. The pleopodal fecundity again showed a linear relationship ($r^2 = 0.8836$, $P < 0.0000$) to the body length (Figure 2). The estimated pleopodal fecundity was 10% lower than the estimated ovarian fecundity calculated by the resulting linear equations. However, we did not find a significant difference between ovarian and pleopodal fecundity when tested by ANCOVA using size as a covariate.

The proportion of eggs placed on each pairs of pleopods and results of the pairwise comparison between different pairs are shown in the Table 1. We found a statistically significant difference ($P < 0.01$) between the egg numbers carried on individual pairs of pleopods. The highest numbers of eggs were placed on the 3rd and 4th pair of pleopods with 53.1 ± 23.1 (25-122) and 59.0 ± 24.1 (28-117) eggs, respectively. Practically no eggs were placed on the 1st pair of pleopods: 1.6 ± 1.5 (0-5) eggs. Altogether, 15.2 ± 7.8 (1-31) eggs were attached directly to the abdomen cuticle. The average size of eggs attached to the pleopods was 1.8 ± 0.21 mm (1.45-2.15 mm). We did not find any relationship between the size of a female and the size of eggs.

Table I

Percentage of eggs carried on individual pairs of pleopods (different alphabetic superscripts show significant differences in pairwise comparison; $P < 0.01$).

Tableau I

Pourcentage d'œufs incubés sous chaque paire de pléopodes

| | 1 st pair | 2 nd pair | 3 rd pair | 4 th pair | 5 th pair | Others | Total no. of eggs |
|-------------------|--------------------------|---------------------------|----------------------------|---------------------------|---------------------------|--------------------------|-------------------|
| Average \pm STD | 1 \pm 0,6 ^e | 18 \pm 2,7 ^c | 25 \pm 1,8 ^{ab} | 27 \pm 2,4 ^a | 22 \pm 3,2 ^b | 7 \pm 2,7 ^d | 217,8 \pm 94,93 |
| Min-Max | 0-2 | 14-24 | 21-27 | 23-32 | 16-27 | 1-11 | 95-492 |

Table II

The size of females, fecundity and egg/juvenile size (average and range).

Tableau II

Longueur des femelles, fécondité et taille des œufs/juveniles (moyenne et amplitude).

| | Females | | | No. of eggs/ juveniles | | Egg/juvenile size | |
|--|---------|-----------------|------------|------------------------|--------|-------------------|------------|
| | No. | body lenth (mm) | range (mm) | average | range | average (mm) | range (mm) |
| Ovarian fecundity | 20 | 54.1 | 43-93 | 130.8 | 46-505 | 1.2 | 0.9-1.7 |
| Pleopodal fecundity | 16 | 66.8 | 47-96 | 217.8 | 95-492 | 1.8 | 1.4-2.1 |
| Juveniles at the 3 rd stage | 14 | 65.6 | 47-88 | 135.7 | 15-243 | 7.1 | 6-8 |

Juveniles at the 3rd stage

All 20 females laid eggs between April 22 and May 15. Six females lost eggs during the incubation. Juveniles hatched between June 11 and June 24, and moulted to the 3rd stage between June 22 and July 4. Total number of juveniles per female at the 3rd stage (calculated from the values of 14 females which had not lost eggs) was 135.7 ± 67.24 . The body length and weight of the 14 females was 65.6 ± 10.92 mm (47-88 mm) and 9.14 ± 4.73 g (2.50-18.68 g), respectively. The number of juveniles showed a positive correlation with the female body length ($r^2 = 0.6562$, $P < 0.0004$) (Figure 2).

Time of embryonic development

The body length and weight of 80 mature females used in the experiment was 56.8 ± 10.06 mm (41-82 mm) and 5.91 ± 5.60 g (2.10-17.91 g), respectively. The time of laying was not dependent on the size of the female. We did not confirm that larger females extruded their eggs earlier. The disturbance also caused considerable losses of eggs during the incubation, especially if female was disturbed directly during the laying process. Only 43 females out of 80 females laid their eggs, and 26 of them reached the 1st juvenile stage. The laying of females in this experiment took place between April 18 and May 16. Hatching of juveniles occurred between June 12 and June 27. The mean time from laying to hatching of juveniles at the 1st stage was 46 ± 3.8 days (37-56 days), i.e. 647 ± 39.9 CTU (543-730 CTU). The water temperature slowly increased during the experiment from 8 to 17°C. Females laying the eggs later had a lower requirement of CTU for embryonic development.

DISCUSSION

The higher fecundity of spiny-cheek crayfish in comparison with native European crayfish was confirmed. The ovarian fecundity of 130.8 ± 107.63 (46-505) oocytes per female is in agreement with our previous study (KOZÁK and POLICAR, in press). STYPIŃSKA (1973) presented an even higher average ovarian fecundity for the spiny-cheek crayfish, from 315 to 440 oocytes. Our results are comparable, however, if we take into account the size of females used in the experiments. The impact of spiny-cheek crayfish female size on fecundity has been confirmed by several studies, e.g. PIEPLOW (1938), STYPIŃSKA (1973), SCHULZ and ŠMIETANA (2001).

The literature data about average pleopodal fecundity of spiny-cheek crayfish are wide, ranging from 139 to 440 eggs per female, and there is always a large difference between minimum and maximum (altogether, the pleopodal fecundity ranges in the interval 35-555 eggs) (PIEPLOW, 1938; HOLDICH and LOWERY, 1988; STUCKI, 2002; HAMR, 2002). The pleopodal fecundity of 217.8 ± 94.93 (95-492) eggs recorded in our experiment is in agreement with the published data. We did not find a significant difference between ovarian fecundity and pleopodal fecundity observed just after laying when the results were corrected for female size. We can presume that the potential difference between ovarian fecundity and the number of pleopodal eggs at the end of embryonic development are caused mainly by losses of eggs during the incubation period. The magnitude of this difference may possibly reflect quality of environmental conditions. This phenomenon has already been observed in the spiny-cheek crayfish by PIEPLOW (1938), and by e.g. CELADA *et al.* (2005a,b) and SÁEZ-ROYUELA *et al.* (2005) in other crayfish species. We also recorded large variability in the fecundity of females of a comparable size, similarly to HARLIOĞLU *et al.* (2004).

The spiny-cheek crayfish has a higher average fecundity than native European crayfish, and comparable to non-native American species present in Europe. SAVOLAINEN

et al. (1996) presented an average ovarian fecundity for the noble crayfish and signal crayfish of 166-264 oocytes with a minimum of 73 and maximum of 436 oocytes, and 377-456 (73-952) oocytes, respectively. They presented pleopodal fecundity of only 50-60% (max. 250 eggs) and 30-60% (max. 466 eggs) of ovarian fecundity for the noble and the signal crayfish, respectively. These observations, however, were carried out in spring rather than close to the egg laying time. For the signal crayfish, CELADA *et al.* (2005a) presented an average pleopodal fecundity of up to 348 and 233 eggs at the beginning and at the end of embryonic development, respectively. STYPIŃSKA (1973) presented 130-325 and 210-345 oocytes for the noble crayfish and the narrow-clawed crayfish, respectively, dependent on the size of females. SCHULZ and ŠMIETANA (2001) presented that fully-matured female spiny-cheek crayfish had a considerably higher number of eggs than narrow-clawed crayfish of the same body length. This difference amounted to approx. 200 eggs for females of 9 cm length and 300 eggs for females of 11 cm length. LINDQVIST and LOUEKARI (1975) presented 248 oocytes for the noble crayfish. STUCKI (2002) presented the following average pleopodal fecundities per female: noble crayfish 150, stone crayfish 60, narrow-clawed crayfish 180 and signal crayfish 114 eggs per one female. MAGUIRE *et al.* (2005) founded a mean pleopodal fecundity of 62 eggs, ranging between 30 and 104 eggs, for the stone crayfish. The big eggs losses happen during the winter incubation among these crayfish species (CELADA *et al.*, 2005a,b), which is a significant advantage for the spiny-cheek crayfish, which carries eggs for one to two months only in spring (as described already by ANDREWS, 1907).

BRINK *et al.* (1988) recorded ovigerous females of the spiny-cheek crayfish in their studied catchments from March to May. In our experiment, females carried eggs in April and May, and the mean time from laying to hatching was 46 ± 3.8 days (37-56 days, i.e. 647 ± 39.9 CTU (543-730 CTU). This is much lower than for the noble crayfish, where the estimated requirement for hatching in nature is approximately 240 days (1,500 CTU), (CUKERZIS, 1973; TAUGBØL and SKURDAL, 1990). MASSON (1977), HOFMANN (1980), WINNICKI *et al.* (2004), and CELADA *et al.* (2005a,b) stated that 906-1,380 CTU are needed for embryonic development in the signal crayfish, which is still higher than values recorded in our experiment for the spiny-cheek crayfish. The requirement of higher CTU for egg development in European crayfish in comparison with the spiny-cheek crayfish is evident even if we take into account the artificially shortened incubation times under laboratory conditions (HESSEN *et al.*, 1987; PÉREZ *et al.*, 1998; CARRAL *et al.*, 2004; POLICAR *et al.*, 2004).

The number of juveniles reaching the 3rd stage was also high (136 juveniles) in comparison with the noble crayfish and the signal crayfish at the 2nd stage (stage of independence). However, the number of juveniles in the 2nd or 3rd stage per female under laboratory conditions is mainly related to rearing conditions, so the differences of such values among various studies are difficult to interpret. In our previous study, under similar experimental conditions we obtained values of 47-97 and 133 juveniles at the 2nd stage for the noble crayfish (POLICAR and KOZÁK, 2002, POLICAR *et al.*, 2004) and the signal crayfish (POLICAR and KOZÁK, 2002), respectively.

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