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Life history, secondary production and population dynamics of *Gammarus fossarum* (Koch, 1836) in a constant temperature stream

Pavel Beracko[1], Anna Sýkorová[1] & Andrej Štangler[2]

[1]*Department of Ecology, Faculty of Natural Sciences, Comenius University, B-2 Mlynská Dolina, SK-84215 Bratislava, Slovakia; e-mail: beracko@fns.uniba.sk*
[2]*Slovak Water-Resource Company, Administration of River Danube Basin, Karloveská 2, SK-84217 Bratislava; Slovakia; e-mail: andrej.stangler@svp.sk*

Abstract: Population of the freshwater amphipod *Gammarus fossarum* was investigated in a calcareous stream with almost constant temperature (7–8 °C) in the Chočské Vrchy Mts (West Carpathians, Slovakia). Quantitative samples of *G. fossarum* taken during 2005 showed population densities varying from 100 m^{-2} in August to 585 m^{-2} in late November. The population was split into juveniles, mature males, mature females without eggs and females with eggs. The percentage of juveniles (40–64%) was always the highest of any of the categories. Ovigerous females occurred throughout the year. The mean sex ratio was 1 : 2.4 (male: female), although its values varied considerably with the time of year. Breeding was continuous, although juvenile recruitment peaked in early spring, summer and early winter. Three discrete cohorts were distinguished from the size frequency distributions. The life span was 6–7 months and the individuals matured approximately in the half of life cycle. The mean fecundity was 9.6 embryos per brood. Variation in fecundity was mostly explained by size of the incubating females. The absolute growth of this species was best described by the Gompertz growth function. Relative growth rates (% body DM day^{-1}) fluctuated in a nonlinear manner with size and age. The highest values of daily growth (2–4% of dry mass per day) were noted approximately in the half of life cycle. Annual production, estimated by the size-frequency method, was 1618.9 g dry mass m^{-2} and P/B ratio was 5.15.

Key words: Amphipoda; life cycle; cohort splitting; sex ratio; eggs

Introduction

One of the most important aspects for understanding freshwater ecosystems is the biology of the species that live in them. In this context, the study of the life history of single species is essential in order to achieve a full knowledge of the ecosystem itself and the relations within it. Many studies have tried to reach this goal through generalizations taken from the study of a reduced number of species, assuming that the rest of the members of their genus or family behave in the same manner. As pointed out by several authors (Zwick 1981; Stewart & Stark 1993), this is neither a good approximation nor an appropriate basis for ecological studies, and particular studies must be carried out in order to fulfil this lack of information. Furthermore, these studies must be developed in different habitats with particular characteristics, such as temporary streams, saline streams, streams with constant temperature, etc., in order to characterize the key factors that influence the life history of the organisms in a given environment. The species *Gammarus fossarum* (Koch, 1836) is the most frequent species of gammarids in freshwater stream of mountainous areas of central Europe (Pöckl et al. 2003) and plays a major role in the breakdown of leaf litter. Because *G. fossarum* is so widespread, frequently abundant, an important and obvious member of most freshwater communities, it has been extensively studied from a variety of viewpoints. The differences between environmental conditions of streams, where the *G. fossarum* successfully survives, are considered to be the explanation for differences in life history and population dynamics of this species (Goedmakers 1981; Pöckl & Humpesch 1990). Pöckl et al. (2003) found out, that water temperature has a dominating influence on life history, reproduction and growth of *G. fossarum*. There are a large number of investigations undertaken on *G. fossarum* biology, such as breeding (Obrdlík 1972; Goedmakers 1981; Pöckl & Humpesch 1990; Pöckl 1993; Pöckl et al. 2003), preference of habitat (Helan et al. 1973; Goedmakers 1981; Zavadilová 2007), temperature effect on the sex ratio (Pöckl et al. 2003), feeding behavior (Pöckl 1995; Dangles & Guérold 2000), population composition (Helan et al. 1973; Goedmakers 1981), growth rate and production (Helan et al. 1973; Pöckl 1995).

Whereas according to several authors, the water temperature is the main factor controlling autecological and population characteristics of *G. fossarum*, the aim of our study was to characterize the life history

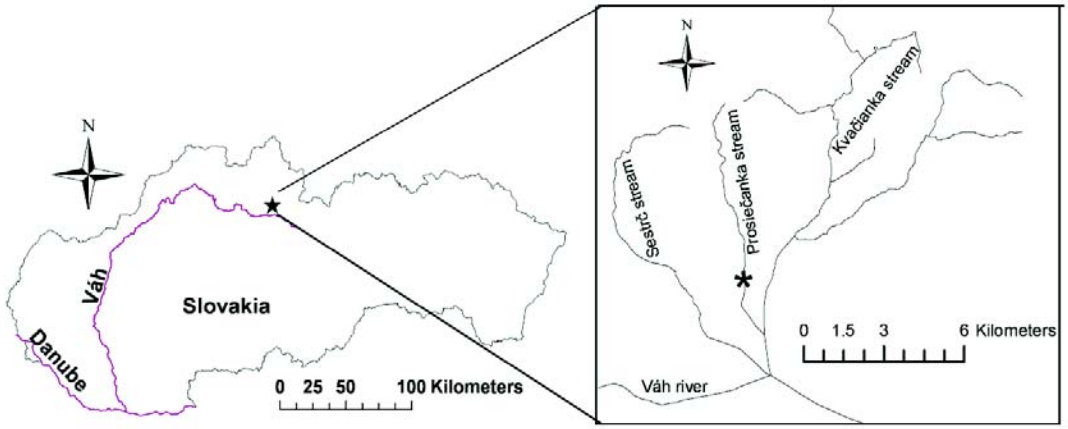

Fig. 1. Location of sampling site. * – sampling site

and population dynamics of this species in a particular habitat with constant temperature through the year and so water temperature does not control the sequence of events.

Material and methods

Study area

The study was carried out in Prosiek stream, located in Chočské Vrchy Mts (West Carpathians), in the northern part of Slovakia (GPS coordinates: 49°09′43.49″ N, 19°29′32.2″ E, altitude: 705 m a.s.l.) (Fig. 1). The sampling site is located about 100 m below spring. The spring temperature is almost constant through the whole year (7–8 ℃). The mean (± standard deviation) length of daylight is 12.3 (± 2.7) hours. The geological substrate, formed by limestone, is reflected in high water pH values (pH 7.98).

Sampling and data analyses

The quantitative samples (2 samples from mesolithal and 2 from macrolithal, representing a total area of 0.4 m^2) of macrozoobenthos were collected monthly, from January to December 2005, using a Kubíček's benthic sampler (area 0.1 m^2, mesh size 0.5 mm). Collected material was preserved in 4% formalin. In the laboratory, the specimens of *G. fossarum* were separated from the remaining macrobenthos. Total length (from rostrum to telson) of all individuals was measured with the aid of a micrometer fixed to the binocular of a microscope to the nearest 0.5 mm. The length of life cycle and cohorts were identified on the basis of the size-frequency histograms, where the individuals were grouped into 1.0 mm size classes. The amphipod individuals were separated according to Goedmakers (1981). Adult individuals were distinguished by the presence of genital papillae (males) and oostegites (females). Adult females were divided into the following groups: females without eggs and embryos and females bearing eggs and embryos. In the absence of secondary sexual dimorphic features, the individuals were recognized as juveniles. Estimation of individuals mass was made according to Burgherr & Meyer (1997) using the equation:

$$\ln \mathrm{DM}\ (\text{dry mass}) = \ln a * b \ln L\ (\text{length})$$

where for *Gammarus fossarum*: $\ln a = -4.95$, $b = 2.83$. For growth analysis three growth models were tested: Exponential, Bertalanfy and Gompertz. The Gompertz growth model was chosen as the best fitting: $Y = A + C * \exp(\exp(-B * (X - M)))$, where: Y – body dry mass, X – time, A – the lower asymptote, C – the upper asymptote, M – the time of maximum growth, B – the growth rate. The individual daily growth rates G (individual mass day^{-1}) (Waters 1977) was estimated by using an exponential relationship between the log-transformed values of the mean individual dry mass for each date over time:

$$G = 100 * (\ln(M_{i+1}/M_i)/t)$$

where M_i – mean individual mass at time i, M_{i+1} – mean individual mass at time $i+1$, t – the time interval in days. Secondary production was evaluated using the size-frequency method (Benke 1979):

$$P = [I \sum_{j=1} (n_j - n_{j+1}) * (w_j + w_{j+1}) * 1/2] * 365/\mathrm{CPI}$$

where: I – the number of size classes, n_j – the mean number of individuals in size class j, n_{j+1} – the mean number of individuals in size class $j+1$, w_j – the mean dry weight of an individual in the j-th size class, w_{j+1} – the mean dry weight of an individual in the j-th+1 size class and CPI – the cohort production interval in days. The monthly productions were estimated according to Beracko (2007) using the equation:

$$P_i = \sum_{j=1} (P_j * N_{ij}/N_j)$$

where P_i – production of the population in the i^{th} month, P_j – production in the j^{th} size class (this production is known from the size-frequency method), N_{ij} – number of individuals in the j^{th} size class and in the i^{th} month, N_j – total number of individuals in the j^{th} size class. The regression between body length of females and the number of eggs they carried was performed with Statgraphics centurion XV software. The growth models were created and tested in GenStat 12 software. The variations of the individual growth rate and production in relation to the length of day-ligth were analysed with a Spearman's rank correlation test in Statgraphics centurion XV software.

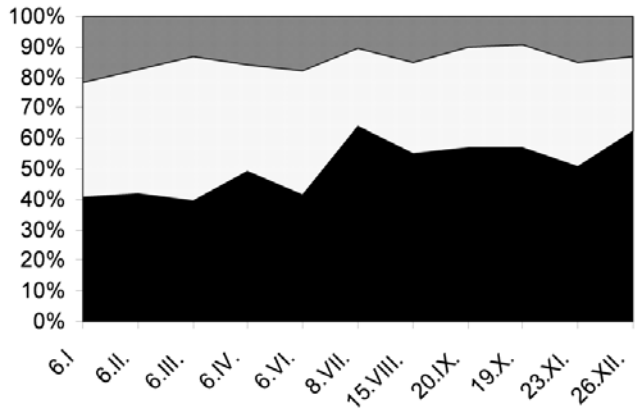

Fig. 2. Monthly variation in the percentages of juveniles (■), females (□) and males (▩) of *Gammarus fossarum* at the sampling site.

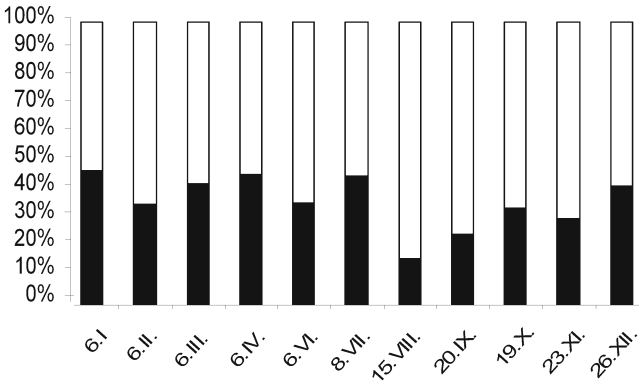

Fig. 4. Monthly variation in the percentages of adult females of *Gammarus fossarum* with eggs and in those without eggs (■ – females with eggs, □ – females without eggs).

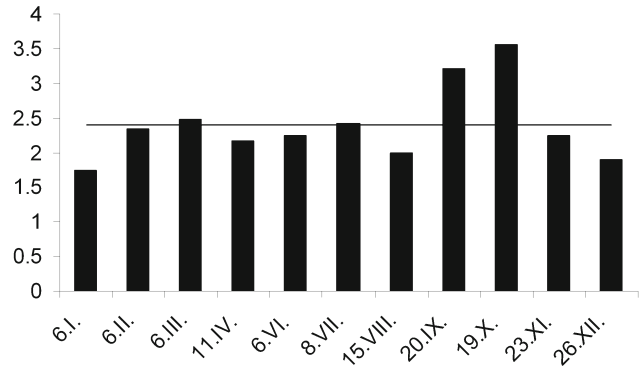

Fig. 3. Monthly variation in the sex ratio of *Gammarus fossarum* (number of females per male, — mean value).

Results

Population structure

A total of 1,350 individuals were collected in the sampling area through the whole studied period. The mean (± standard error) population density of *G. fossarum* was 329 (± 66) ind. m^{-2} (the highest density was in November – 595 ind. m^{-2} and the lowest one was in August – 100 ind. m^{-2}). The juveniles had high proportion in the population throughout the year. Their captured frequency ranged from 40% in January to 64% in July (Fig. 2).

The monthly variation in the sex-ratio (number of females/number of males) is shown in Fig. 3. The mean value (± standard error) of the sex-ratio was 2.39 (± 0.54). The highest and lowest sex ratio values were found in October (3.55 females/male) and in January (1.74 females/male), respectively.

Gravid females were found throughout the year. The percentage of the gravid females in the total number of adult females was the lowest in August (18%), but in the next four months the percentage of the females with eggs gradually increased to the level around 40% as it was in the first seven months of the year (Fig. 4).

Life cycle and reproduction parameters

In the study area, the individuals of *G. fossarum* had a 6–7 month life cycle. Breeding and newly hatched individuals occurred in the population throughout the year, but there were three pronounced peaks of newly hatched individuals – three main cohorts were identified in the population during the annual cycle (Fig. 5). The

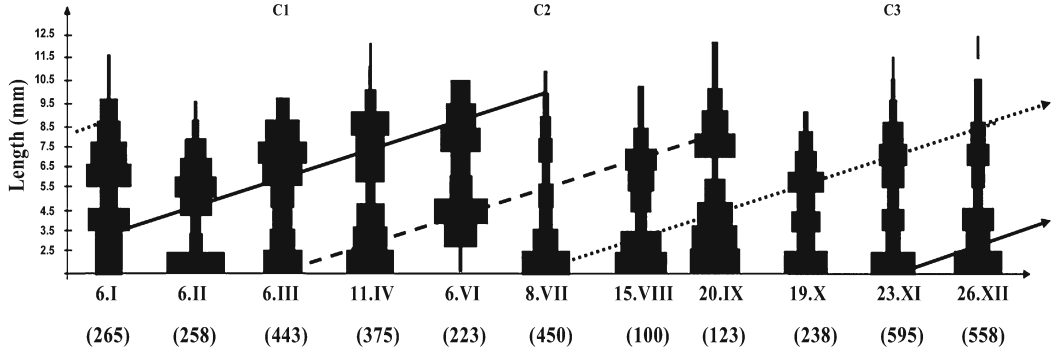

Fig. 5. The size – frequency distribution of *Gammarus fossarum*. The width of each box represents the relative abundance of individuals. The numbers in parentheses represent the absolute number of individuals per 1 m^2 in each month. The lines indicate the development of cohorts (– – – C1, ··· C2, — C3).

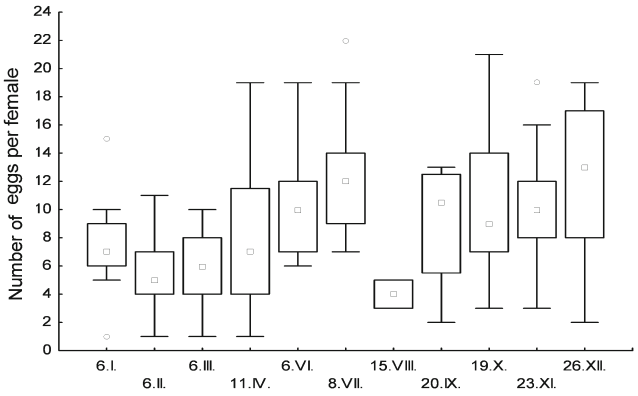

Fig. 6. Monthly variation in the number of eggs per gravid female of *Gammarus fossarum*. For each month sample, the mean value, 25% to 75% quartiles, minimum and maximum number of eggs per gravid female are shown.

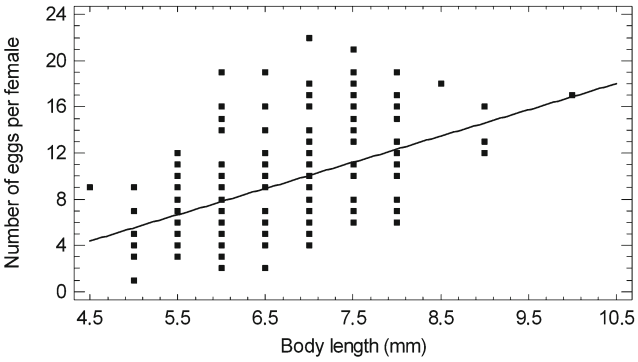

Fig. 7. Relationship between number of eggs and body length in gravid females of *Gammarus fossarum*.

spring cohort (C1) was produced from winter cohort (C3) of the previous year. The individuals of cohort C1 hatched from February to March and they occurred to late September. The summer cohort (C2), extended from July to January of the next year, was produced from cohort C1. The cohort C3 appeared in population in late November and it was produced from cohort C2.

Reproduction parameters

The body length of adult females was greater than 4.5 mm and for adult males it was greater than 5 mm. The number of eggs per brood ranged from 1 to 22 (mean ± standard error – 9.6 ± 4.5 eggs per brood). The highest mean number of eggs per female was found out in July (12.6 ± 3.9) and in December (12.6 ± 4.7) (Fig. 6). In these months the mean body length of gravid females was also the highest. Linear regression was used to fit the relationship between the number of eggs per brood and female body length (Fig. 7). This relationship is defined by the equation: number of eggs per brood = –5.81 + 2.27∗female body length (F = 67.3; $P < 0.01$; $R^2 = 26.6\%$).

Individual growth and production

The growth of *G. fossarum* was described best by the Gompertz growth function (Table 1). Absolute (incremental) growth rates fluctuated in a nonlinear manner with size and age, and were maximal around the inflection point (C1 – 166th day of life, C2 – 123th day of life, C3 – 96th day of life). The growth curve of each cohort is given in Fig. 8.

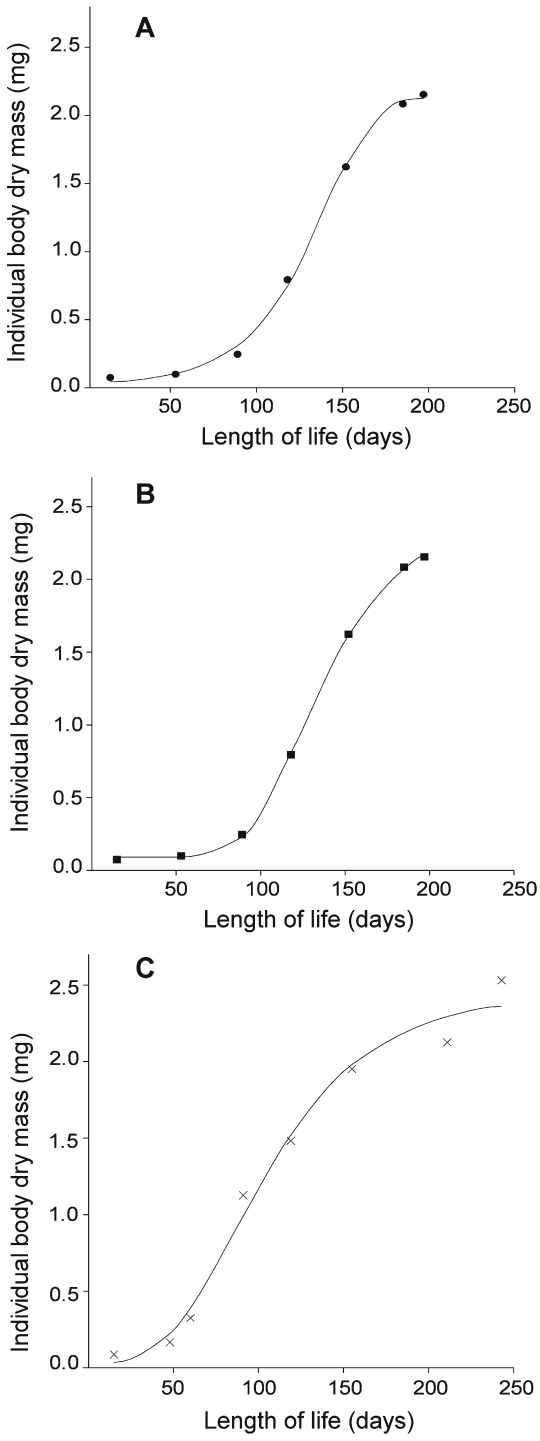

Fig. 8. The Gompertz growth curve of individuals of each single cohort of *Gammarus fossarum*. a – cohort 1 (C1), b – cohort 2 (C2), c – cohort 3 (C3).

The relative (instantaneous) growth rate (G, % body dry mass per day) markedly varied through the life cycle. At the time, when the daily mass increment was the highest, the individuals increased their mass

Table 1. The Gompertz growth functions of each cohort of *Gammarus fossarum* in the sampling site.

	Gompertz growth curve $Y = A + C * e^{-e^{(-B*(X-M))}}$	F statistic	Significance level	Coefficient of determination (R^2)
Cohort 1	$Y = 0.14 + 2.56 * e^{-e^{(-0.02*(X-147))}}$	191.39	$P < 0.01$	0.99
Cohort 2	$Y = 0.09 + 2.31 * e^{-e^{(-0.03*(X-123))}}$	308.66	$P < 0.01$	0.99
Cohort 3	$Y = 0.02 + 2.40 * e^{-e^{(-0.02*(X-96))}}$	94.14	$P < 0.01$	0.97

Explanations: Y – body dry mass, X – time, A – the lower asymptote, C – the upper asymptote, M – the time of maximum growth, B – the growth rate.

Table 2. Monthly variation in mean length of day-light, in production of *Gammarus fossarum* and in relative growth rate (G, % body dry mass per day) of individuals of each cohort at the sampling site.

Period (month/day)	Day-light length (hour)	Production (mg DW m^{-2})	Daily growth – G (%)		
			Cohort_1	Cohort_2	Cohort_3
01/06–02/06	8.7	133.72			2.01
02/06–03/06	9.8	67.79			3.98
03/06–04/11	10.3	182.53	▼ 0.74		0.76
04/11–06/06	14.4	209.36	2.54		0.15
06/06–07/08	15.1	124.96	2.10		0.55
07/08–08/15	13.2	139.07	4.05	▼ 1.83	
08/15–09/20	12.7	32.73	0.76	1.57	
09/20–10/19	12.4	78.12	0.28	1.96	
10/19–11/23	9.6	44.70		2.07	
11/23–12/26	8.4	318.53		1.29	▼ 1.97
12/26–01/06	8.4	287.40		0.30	1.63

Explanations: ▼ – the beginning of the cohort life.

Table 3. Population and cohort mean density, mean biomass, production and P/B ratio, as well as cohort production interval (CPI), of *Gammarus fossarum* during the annual cycle at the sampling site.

	Annual	Cohort_1	Cohort_2	Cohort_3
Mean density (ind. m^{-2})	322	97	179	217
Mean biomass (mg DW m^{-2})	314.09	61.80	114.04	138.25
Production (mg DW m^{-2})	1618.90	309.31	556.87	751.79
P/B ratio	5.15	5.01	4.88	5.44
CPI	–	227	197	228

by 4.05% (C1), 2.07% (C2) and 3.98% (C3) every day (Table 2). We found no correlation between monthly individual growth rate and mean monthly day-light ($R = 0.02$; $P < 0.05$).

The annual production of *G. fossarum* was 1618.9 mg DM m^{-2}, with an annual turnover biomass ratio (P/B) of 5.15 (Table 3). The monthly production values ranged between from 32.73 mg DM m^{-2} (August – September) to 318.53 mg DM m^{-2} (December) (Table 2). We found out three peaks (March, July and December) of production during the year. The cohort production values were 61.80 mg DM m^{-2} for the cohort 1, 114.04 mg DM m^{-2} for the cohort 2 and 138.25 mg DM m^{-2} for the cohort 3. The cohort P/B ratio ranged from 4.88 to 5.44 and the highest value was found in individuals of winter cohort (C3) (Table 3). Monthly production values were negatively correlated with mean monthly day-light ($R = -0.29$; $P < 0.05$).

Discussion

Temporal change in the density, with three peaks in spring, summer and autumn – winter was observed in a population of *Gammarus fossarum*. The monthly variation in population density of *G. fossarum* was most probably affected by its life cycle; it sharply increased following the recruitment of the spring, summer and winter cohorts but small recruitment of *G. fossarum* juveniles was practically continuous throughout the year. Reproduction in amphipods usually occurs throughout the year (the main reproduction period – from early spring to early autumn) beside winter (Rowshan 1991; Zielinsk 1998; DeMarch 1981; Stürzbecher et al. 1999; Maranhão & Marques 2003; Ladewig et al. 2006). Low temperature extends maturation period (de March 1981) and increases mating and fertilization time (Maranhão et al. 2001; Sutcliffe 1992). In our case, the temporal changes in the percentage of the ovigerous fe-

Table 4. Comparison of individual and population characteristics of *Gammarus fossarum* from different water habitats.

Stream	Water temperature (°C)	Life span (days)	Maturation age (days)	Hatching time of individuals (month)	Percentage of juveniles	Sex ratio (females/male)	Fecundity (eggs/female)	Citation
Salzbach	7.5	(775–850)	402	A–MJ, JL-S	–	–	–	Pöckl et al. (2003)
Leitha	9.6	(515–645)	290	A–MJ, AU-O	–	–	–	Pöckl et al. (2003)
Voekla	11.5	(453–514)	213	MJ–JN, S-O	–	–	–	Pöckl et al. (2003)
Slack	11.1 (6.2–16.8)	–	–	JN–JL, S	(5–60%)	0.98	12.1	Goedmakers (1981)
Lušová	– (0–18)	–	–	M–A, JL–AU	(40–50%)	(1.4–2.5)	–	Helan et al. (1973)
Granický brook	10.5 (2–15.2)	(365–455)	–	MJ–JL	(10–90%)	(0.7–1.5)	15.5 (1–30)	Pařil (2011)
Prosiečanka	7–8	(150–180)	(90–120)	all year	(40–60%)	(1.7–3.5)	9.6 (1–22)	this study

Explanation: value without parentheses is mean of parameter; values in parentheses are range of parameter.

males confirm that the population was sexually active throughout the year. The constant water temperature probably results in the addition of one main cohort – the winter cohort. The same reproduction behavior was found in *G. pulex*, the reproduction period was continuous and the lower temperature in winter (about 2 °C comparing to other seasons) caused 25 percent reduction in reproduction rate (Mohammadi et al. 2010). The proportion of juveniles was relatively constant in the population throughout the year. This constant proportion is probably a result of the continuous hatching of new individuals. Goedmakers (1981) observed the variation in proportion of juveniles in *G. fossarum* from 2 to 60 percent. In this case, the mean (± standard deviation) water temperature was 11.1 (± 3.1) (Goedmakers 1980).

In the study area, the sex ratio of *G. fossarum* was always in the favour of females (from 1.74 females/male to 3.55 females/male). Sex ratio differs from a species to another and even in same species in different climates (Mohammadi et al. 2010). Differences in sex ratio have been frequently observed among different population of *G. fossarum*. Helan et al. (1973) observed a dominance of males in *G. fossarum* throughout the year. Goedmakers (1981) found that the sex ratio in *G. fossarum* was approximately 1:1 with only small variations during the year. In both previous cases, the streams had thermal regime typical for submontane streams of middle latitude with temperature variation 0–18 °C. Temperature and photoperiods are the most important factors that can affect sex ratio. For example, the long daylight (over 14 hours) increases male production in *Gammarus duebeni* Liljeborg, 1852 by 25%, while female hatching is more frequent in shorter daylight periods (Bulnheim 1972; Watt 1994; Dunn 2005). Prato & Biandolino (2003) found out the same result in sex ratio of *Gammarus aequicauda* (Martynov, 1931). The sex ratio variation in *Uhlorchestia spartinophila* Bousfield et Heard, 1986 was influenced by differential mortality caused by seasonal changes in quality or availability of food (Kneib 1997). Confirming many studies, the gammarid females are more numerous than males in winter, when daylight is shorter and temperature is lower, and conversely, the proportion of males increases mainly in warm season. Cytochrome P450 aromatase is an enzyme that catalyzes the conversion of androgens to estrogens and plays a role in temperature-dependent sex determination (Simpson et al. 1994). In most of the thermosensitive fish species, the higher water temperature blocks of estrogen biosynthesis using aromatase inhibitors and it results in partial or complete masculinization (Piferrer et al. 1994; Guiguen et al. 1999), while lower water temperature is associated with strong aromatase gene expression resulting in feminization of the population (D'Cotta et al. 2001). In our case, a pattern can be similar. The constant water temperature about 7 °C probably is responsible for dominant hatching of females and relatively constant sex ratio throughout the year. Some individual and population characteristics of *G. fossarum* from different streams are shown in the Table 4.

The length of life cycle *G. fossarum* was relatively short in the study area. Different thermal regimes of streams subtly affect length of life cycle and growth of gammarids (Pöckl et al. 2003). The length of life cycle of *G. fossarum* was relatively long (>2 years) in the stream with a mean temperature 7.5 °C, whereas in the stream with mean temperature 11.5 °C it was only 14–18 months (Pöckl et al. 2003). Comparing our life span results of *G. fossarum* with Pöckl et al. (2003), significant differences were noted but the times required for growth from birth to sexual maturity was relatively long in the both cases (often occupying 50% or more of the total life span). An increase in the number of eggs per female during development is a common feature of many crustaceans (Davis 1981) and this fact was also confirmed in our study. Kozačeková et al. (2009) found, that stonefly *Protonemura intricata* (Ris, 1902) had bivoltine life cycle at this site, whereas it is usually accepted that *P. intricata* has a simple univoltine life cycle (Zwick 1981; Marten & Zwick 1989).

The growth of all crustaceans occurs in stages, each combined with a moult, at least until sexual maturity is reached (Gruner 1993). Kolding & Fenchel (1979), studying life cycle of gammarid amphipods, observed that the growth rate decreases when they mature and begin to reproduce. We noted the high values of individual daily growth rate in the first half of life span. Pöckl (1995) found under laboratory conditions that growth rates of *G. fossarum* were highest near birth and declined in a monotonic exponential trend with increasing body weight and age at 4 °C and 8 °C. At 12, 16

and 20 °C growth resembled a sigmoid curve, and was optimally described by logistic functions (Pöckl 1995). In our case, the individuals reach the inflection point at 7 °C, and growth was described the best by Gompertz growth functions. The highest individual growth rate of *G. fossarum* was 7.98% wet weight day^{-1} at temperature range 3.8–20.2 °C (Pöckl 1992). In our case, the maximal individual growth rate was 4.05% dry weight day^{-1}.

The secondary production of *G. fossarum* in the Prosiečanka stream was similar as Iversen & Jessen (1977) found in *G. pulex* in the headwater streams. On the other hands P/B ratios were significantly different. The individuals of *G. fossarum* had 2.5 times higher biomass turnover than it was found in *G. pulex*. Griffith et al. (1994), in a study of shredder production in headwater streams in West Virginia, estimated annual production of *G. minus* at 2.43 g DM m^{-2}. Helan et al. (1973) estimated secondary production and P/B ratio of *G. fossarum* in submontane stream Lušová as 10.62 g wet mass m^{-2} and 4.2, respectively. The annual P/B ratios ranged from 4.1 to 6.2 for the univoltine amphipods (Waters 1977). The present P/B ratio is well within this range but the population of *G. fossarum* was trivoltine. The explanation of the difference in gammarid production and P/B ratio values are in some aspect of the habitat, such as food sources, spatial parameters, temperature, or water chemistry is responsible for the difference in production (Haley 1997).

Conclusion

The present study in a particular habitat lets us examine how a population of *G. fossarum* behaves when the sequence of events in the life cycle is under the control of constant water temperature. The type of thermal regime seemed to be important in regulating breeding, determining the life-history pattern and some population characteristics of *G. fossarum*. Constant water temperature (7 °C) probably allows individuals continuous breeding and hatching of winter cohort leading to an unusual life strategy of the population, different from many other localities, that consists of three main cohorts during the year. The sex ratio was considerably different than that previously noted in other populations. The absence of temperature fluctuations and water temperature of about 7 °C determine most likely the hatching predominant of females.

Acknowledgements

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