

Life history and reproductive capacity of *Gammarus fossarum* and *G. roeseli* (Crustacea: Amphipoda) under naturally fluctuating water temperatures: a simulation study

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SUMMARY

1. Mathematical functions developed in long-term laboratory experiments at different constant temperatures were combined with daily water temperatures for 1991–93 in eight Austrian streams and rivers to simulate the complex life histories and reproductive capacities of two freshwater amphipods: *Gammarus fossarum* and *G. roeseli*. The functions describe brood development times, hatching success, times taken to reach sexual maturity, growth, and fecundity. The sex ratio was assumed to be 0.5 and an autumn–winter reproductive resting period was based on observations of six river populations. Simulations included summer-cold mountain streams, summer-warm lowland rivers, watercourses fed by groundwater or influenced by heated effluents, and varying amplitudes of change within each year.

2. A FORTRAN 77 computer program calculated growth from birth to sexual maturity of first-generation females born on the first day of each calendar month in 1991, and the numbers of offspring successfully released from the maternal broodpouch in successive broods. At the 1991–93 regimes of temperature, individual *G. fossarum* released 127–208 offspring and *G. roeseli* released 120–169 in seven or eight successive broods during life spans of less than 2 years in six rivers. Life spans extended into a third year in the relatively cool River Salzach (mean temperature 7.5 °C). They were not completed in the very cold River Steyr (mean 5.6, range 2.5–7.9 °C), where *G. fossarum* produced five broods (totalling 120 offspring) and *G. roeseli* only two broods (totalling 28 offspring) in the 3-year period. Except in the Steyr, some offspring grew rapidly to maturity and produced several second-generation broods during the simulation period; in the warmest rivers some third-generation broods were also produced. Birth dates, early or late in the year, influenced the subsequent production of broods and young, depending on temperature regimes in particular rivers. Total numbers of offspring produced by the second and third generations represent the theoretical reproductive capacities of *G. fossarum* and *G. roeseli*. Minimum and maximum estimates mostly ranged from 100 to 17 300, were larger for *G. fossarum* except in the warmest river (March), where temperatures rose above 20 °C for 56–78 days in summer, and largest (maximum 37 600) in the River Voeckla heated by discharge from a power-station (mean 11.5 °C). Results from the simulations agree with preliminary assessments of relative abundances for *G. fossarum* and *G. roeseli* in several of the study

rivers, but in some one or both species appear to be absent. On a wider scale, the present study confirms that *G. fossarum* is potentially more successful than *G. roeseli* in cool rivers but indicates that neither species is likely to maintain viable populations in cold rivers strongly influenced by snow and ice-melt.

3. The potential impacts of future river warming by increases of 1, 2 and 3 °C, due to climate change, vary according to river site, date of fertilisation, the extent of temperature increase, and the species of *Gammarus*. For Austrian rivers with mean temperatures in the range *c.* 7–10 °C, future warming would result in modest changes in the life histories and reproductive capacities of both *G. fossarum* and *G. roeseli*; the former would find improved temperature conditions in watercourses that are currently very cold throughout the year, and both would find warm rivers less tolerable.

4. The high potential reproductive capacity of gammarids, with rapid production of numerous successive broods when sexual maturity is finally achieved, indicates adaptation to high mortality during the relatively long period of growth to sexual maturity, and provides scope for an opportunistic strategy of emigration from centres of population abundance to colonise new territory when conditions are favourable. Rapid expansion of populations is desirable to combat the effects of environmental catastrophes, both frequent and short-term floods and droughts, and more long-term climatic changes that have occurred several times in glacial–interglacial periods during the current Ice Age.

Keywords: climate change impacts, computer simulation, *Gammarus*, life history, naturally fluctuating water temperatures, reproductive potential, running waters

Introduction

The life cycles of commonly studied freshwater species of *Gammarus* are often basically similar, albeit with some variability. They reproduce throughout most of the year but there is a pronounced peak of activity in spring and early summer, and breeding is much reduced in autumn (October–December) when it may cease altogether in some localities as a ‘resting-stage’ intervenes. In contrast to most large freshwater macroinvertebrates, particularly insects, the continuous entry of new individuals into natural populations results in several overlapping generations, making it difficult to identify discrete cohorts (Sutcliffe & Carrick, 1981; Gee, 1988; Pöckl, 1992). Therefore, reproduction and growth have been studied in the laboratory to supplement and interpret observations made on natural populations. Life spans are usually 1–2 years, females may produce six to 10 broods of young, and three generations may be reproducing at the same time in midsummer (Gledhill, Sutcliffe & Williams, 1993; Sutcliffe, 1993).

In freshwater streams of Central Europe, three of the most frequently sampled species of *Gammarus* are *G. fossarum* Koch 1835, *G. pulex* Linnaeus 1758 and *G. roeseli* Gervais 1835. These often occur in the

same geographical region, although *fossarum* chiefly inhabits the central and eastern mountainous areas of Europe, *roeseli* occurs in the lowlands of south-eastern Europe and Asia Minor, and *pulex* is found mainly in the north-western parts of Europe (Karaman & Pinkster, 1977a,b). The species differ in their longitudinal distribution in running waters: *fossarum* tolerates high current velocities and inhabits headwaters and springs, whereas *roeseli* is found in the lower courses of larger rivers. *Gammarus pulex* inhabits springs and upper reaches of small streams where current velocity is low, but in large rivers it occurs mainly in the middle reaches, below those occupied by *fossarum*. However, in some localities two or even all three species coexist in the middle sections of streams (e.g. Besch, 1968; Kinzelbach & Claus, 1977; Pieper & Meijering, 1982; Teichmann, 1982; Janetzsky, 1994). As *pulex* is absent in most parts of eastern Austria, the habitats of *fossarum* and *roeseli* are continuously linked in most of the drainage systems (M. Pöckl, unpublished data).

Laboratory experiments have demonstrated that water temperature has a dominating influence on life history, reproduction and growth of *fossarum* and *roeseli*. There are interspecific differences in brood

development time, egg survival, reproductive success, reproductive resting stage, intermoult intervals, seasonal fecundity, reproductive effort, egg size and growth rates (Pöckl & Humpesch, 1990; Pöckl & Timischl, 1990; Pöckl, 1992, 1993a,b, 1995). The relationships between each of the life-history variables and water temperature have been described by mathematical functions. At 12 °C and above, *roeseli* starts to reach sexual maturity faster and at a larger size, with shorter brood development times and a higher reproductive success, compared with *fossarum*. At a constant 20 °C, *roeseli* attains sexual maturity in 85 days, 11 days sooner than *fossarum*, and these 11 days are exactly the length of time required by the female to develop her first brood (Pöckl, 1992, 1993a,b, 1995). Thus, in lowland rivers of eastern Austria, which exceed 20 °C for 40–80 days each summer, female *roeseli* might produce more offspring and have a higher reproductive capacity than *fossarum*. In streams and rivers where 20 °C is exceeded for only a few days each year or not at all, the reproductive capacity of *fossarum* should be higher than that of *roeseli*. Where temperatures normally do not exceed 10 °C, brood development times, maturation times and life spans are expected to be unrealistically long, so that in reality this cold environment will not be populated by either species.

Some of the above conclusions and speculations were presented as a simple graphical model, based on the survival of eggs to hatching and successful release of young from the maternal broodpouch, at a range of experimental temperatures (Pöckl & Humpesch, 1990). To extend and refine this model, other quantified life-history variables for *fossarum* and *roeseli*, published in work cited above, are incorporated here into a computer-based predictive model. This was used to calculate the specific timing of major events in the life histories of individual females and their offspring for a selected period of time at a natural range of fluctuating temperatures. The latter were specified on a daily basis throughout a 3-year period, based on records for eight large rivers of the Danube drainage system in north-east Austria. Computer simulations were also run for the natural river temperatures augmented by 1, 2 and 3 °C, to examine the potential impact of different degrees of warming as a consequence of possible future climate change (Webb & Nobilis, 1994; Webb, 1996; Conway, 1998; Kerr, 2000).

Preliminary results of sampling for gammarids in the study rivers are also given.

Methods

Water temperatures

Due to the highly diverse physiography of Austria, thermal regimes of streams and rivers show considerable variation. From water temperatures recorded daily at some 200 monitoring stations, data sets covering a 3-year period from 1991 to 1993 were selected for eight river sites (Fig. 1). When simulating the development of *Gammarus*, a minimum of 3 years (1096 days) was necessary in order to include possible life spans of specimens at low temperatures.

Model equations

A FORTRAN 77 computer program was developed, based on known major variables affecting the reproductive biology of *G. fossarum* and *G. roeseli*, and the following series of relationships linking life-history parameters and water temperature were employed. Equations 1–7 are given in linear forms, where a , b , c and f represent constants and \ln represents natural logarithms.

The time required for juveniles to reach sexual maturity (M_t , days) was related to water temperature (T , °C) by a power equation (Pöckl, 1992):

$$\ln M_t = \ln a_1 + b_1 \ln T \quad (1)$$

Mean growth in body wet weight (WWT_t) from birth to old age, for female *fossarum* and *roeseli*, was related to water temperature (T , °C) and time (t , days) by a four-parameter polynomial equation:

$$WWT_t = a_2 T^{t_2} / \{1 + \exp[-b_2 T(t - c_2/T)]\} \quad (2)$$

The number of stage 2 eggs per clutch (N_{EGGS}) was related to body wet weight of females by a power equation:

$$N_{EGGS} = \ln a_3 + b_3 \ln WWT \quad (3)$$

For this relationship, linear and exponential equations were also tested, but power equations provided the best fit to the data. However, there is a tendency towards higher values in spring and lower values in summer.

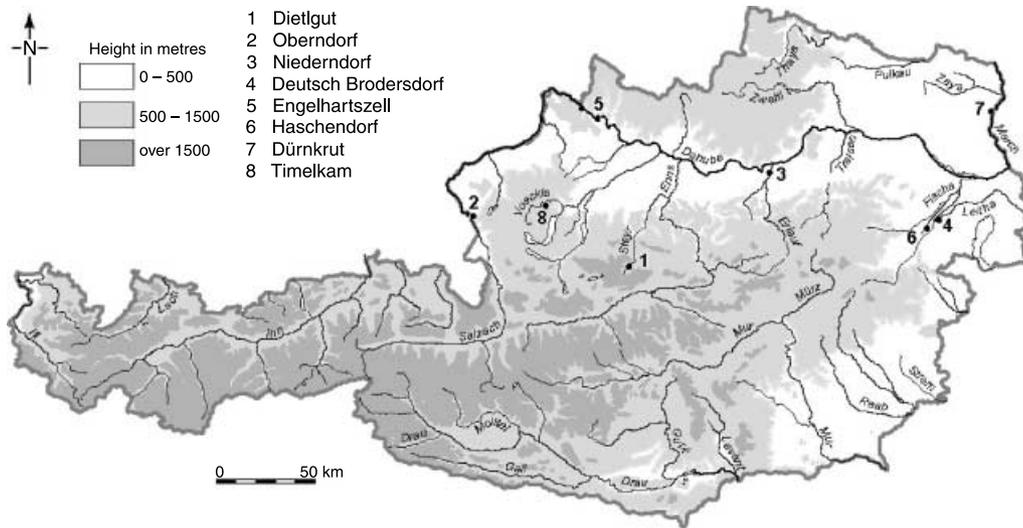


Fig. 1 Locations of the study rivers in Austria.

Egg survival (ES) was related to water temperature by a second-order polynomial function (Pöckl & Humpesch, 1990):

$$ES = c_4 + b_4(T - a_4)^2 \quad (4)$$

Brood development time (d , days) was related to water temperature (T , °C) by a three-parameter model (Pöckl & Timischl, 1990):

$$\ln d = \ln a_5 - [(b_5 \ln T) - c_5 T] \quad (5)$$

The brood development time included a short post-hatching period when hatchlings remained in the female's broodpouch before final release into the water – recorded as the birth date for the brood. The female then moulted and immediately laid a new clutch of eggs into the broodpouch, where fertilisation occurred. In our simulations, development time of this new brood began the following day.

A fecundity index (FI) was calculated by dividing the number of stage 2 eggs (defined by Pöckl, 1993a) per clutch by the wet weight of the corresponding female:

$$FI = N_{EGGS}/WWT \quad (6)$$

The fecundity index was related to experimental water temperature by a second-order polynomial equation:

$$FI = a_7 + b_7 T + c_7 T^2 \quad (7)$$

Computer simulations

For females born on the first day of each month in 1991, calculations were made to estimate the dates when these first-generation females underwent the first adult moult, released their first brood and had subsequent moults and broods. The numbers of offspring produced from each brood were calculated and summed for the life span of nine adult moults. The total numbers of offspring of all daughters (second generation) and granddaughters (third generation, if any) of the original females, produced during 1991–93, were also calculated. For *fossarum* a reproductive resting stage was assumed to last for 2 months, from 1 October to 30 November each year. For *roeseli* the resting stage was assumed to last for 5 months, from 1 October to the end of February. During these periods it was assumed that adult females might undergo a moult but would not immediately mate and start or produce another brood.

Results

Water temperatures

The eight selected data sets represent streams and rivers with widely different temperature regimes in 1991–93 (Fig. 2). The Steyr at Dietlgut was a summer-cold stream with annual mean of 5.6 and 5.7 °C; the

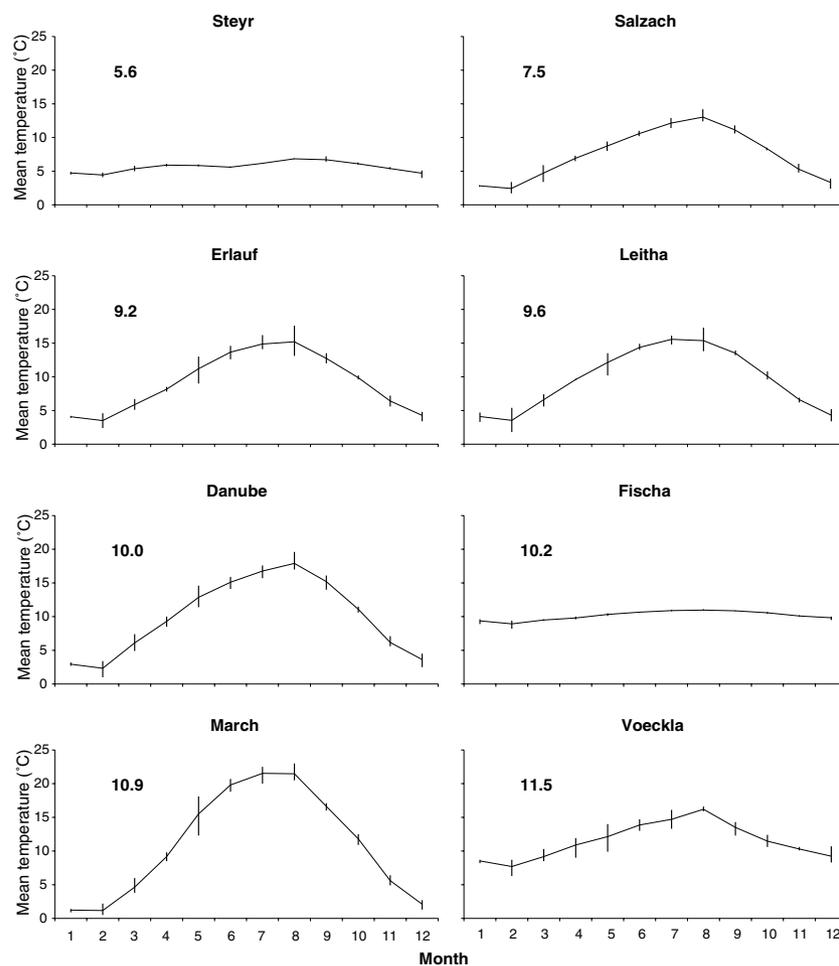


Fig. 2 Average annual thermal regimes (°C) of the study rivers in 1991–93. Mean river temperatures are given as emboldened values; vertical bars indicate the ranges in monthly means during 1991–93.

lowest daily temperature was 2.5 °C and the highest was 7.9 °C. The Fischa at Haschendorf was a typical groundwater-fed stream with a small annual amplitude in temperature, ranging from 6.8 to 11.4 °C, and annual mean of 10.0–10.3 °C. The Voeckla at Timelkam was influenced by thermal discharge from a power station. The annual mean was 11.5 °C; temperatures below 8 °C occurred on 58 days in 1991, on 7 days in 1992 and 6 days in 1993. Temperatures above 20 °C were recorded on 4 days; the highest was 21.9 °C.

The other five streams and rivers showed typical annual cycles. In the Salzach, Erlauf and Leitha, 20 °C was not reached during the study period; annual mean temperatures were, respectively, 7.5, 9.2 and 9.6 °C. In the mainstream of the Danube at Engelhartzell, 20 °C was exceeded on 8 days in 1992, and the mean temperature was 10 °C. The highest annual variations in water temperature (24.3–25.3 °C) were recorded in the River March at Dürnkrot, where annual mean for 1991–93 ranged

between 10.7 and 11.2 °C; 20 °C was exceeded on 56–78 days per year.

Distribution of gammarids

The distribution of *fossarum* and *roeseli* in the eight study rivers is summarised in Table 1. None occurred in the Steyr, a few specimens of *fossarum* only were found in the Salzach, and *roeseli* was also absent from the Erlauf and the Fischa. Both species were relatively numerous in the Leitha but rare in the Danube, which is now occupied by several Pontocaspian gammarids that have invaded the river in the past 50 years. In the mainstream of the Danube, *roeseli* is locally limited downstream from the mouths of summer-warm tributaries.

Simulated life history and growth of females

Table 1 lists the simulated life spans of female *fossarum* and *roeseli*, and Fig. 3 illustrates the calcula-

River	T	<i>G. fossarum</i>	<i>G. roeseli</i>	Status
Steyr	5.6	> 1096	> 1096	F and R absent
Salzach	7.5	775–850	844–897	F rare, R absent
Erlauf	9.2	558–664	602–695	F common, R absent
Leitha	9.6	515–645	528–671	F abundant, R common
Danube	10.0	477–623	466–693	F and R extremely rare
Fischa	10.2	581–602	638–657	F abundant, R absent
March	10.9	415–554	398–475	F absent, R very abundant
Voeckla	11.5	453–514	451–497	F and R present

Variation (range) for individual rivers is due to differing monthly birth dates within the first year of the 1991–93 simulation period. Mean river temperatures (T , °C) are also given. The last column indicates the distribution and status of each species in 2000–01.

Table 1 Simulated life spans (days) and status of *G. fossarum* (F) and *G. roeseli* (R) in eight Austrian rivers; life spans are based on time taken to accomplish nine adult moults

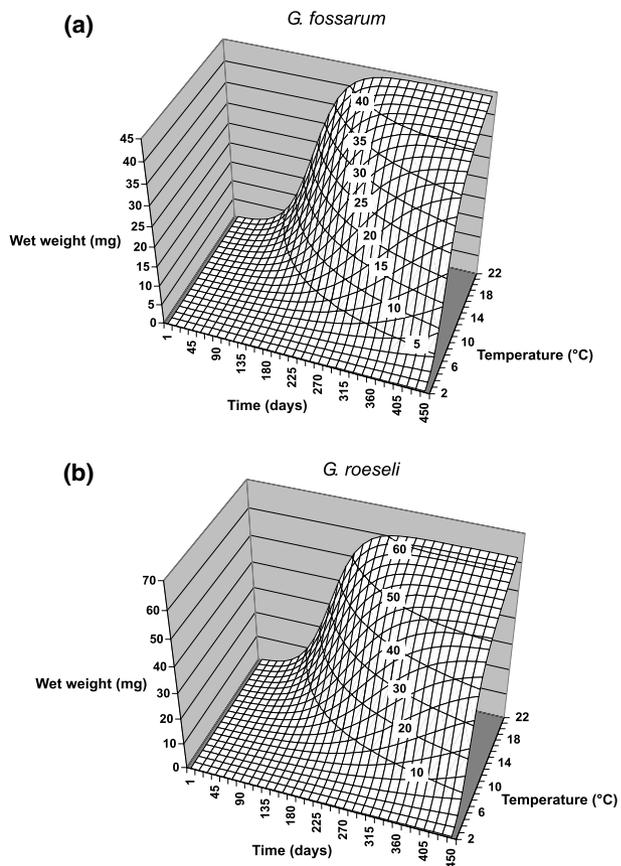


Fig. 3 Calculated growth in body wet weight (mg) of female *G. fossarum* (a) and *G. roeseli* (b) shown against time since birth (age t , in days) and water temperature (T , °C).

ted increases in average body wet weight. From birth to sexual maturity after nine or 10 moults, wet weight increased to *c.* 5 mg in *fossarum* and 10 mg in *roeseli*, and then, respectively, increased to asymptotic maxima of about 41 and 58 mg after another nine moults as adults.

In the cold-water Steyr, neither species completed nine adult moults nor attained the maximum potential body weight within the 3-year simulation period. Hence the life spans of any gammarids living in this river must either exceed 3 years or the females die before completing normal growth through nine moults as adults. Life cycles were also potentially long (>2 years) in the cold waters of the Salzach, but maximum body weights were attained within 3 years.

In the other six rivers in this study, life spans were shortest in the warmest watercourses, March and Voeckla. In the former, where summer temperatures were above 15 °C, life spans were *c.* 13–16 months in *roeseli* and *c.* 14–18 months in *fossarum*, depending on the date (month) of birth. In the Voeckla, where thermal discharges elevated water temperatures during the winter, the range in life spans of both species was slightly smaller, at *c.* 15–17 months. Birth dates had least impact on life spans for gammarids in the Fischa, which had only small annual variations in temperature. Although the mean temperature exceeded 10 °C, relatively cold groundwater entered the Fischa during each spring and summer and this lengthened the simulated life spans of both species by another 1–2 months.

Simulated maturation times and release of broods by first-generation females

The number of days for females to reach sexual maturity, mate and subsequently release their first broods, declined exponentially in the warmer rivers (Fig. 4; Table 2). This maturation time was longest in the Steyr, exceeding 550 days for both species and theoretically taking more than 800 days for *roeseli* born on 1 March 1991. In contrast, females of both

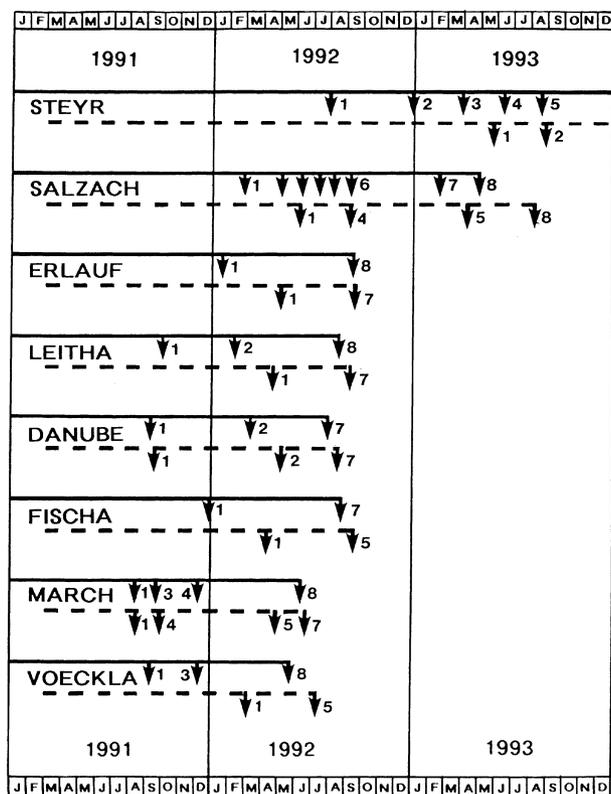


Fig. 4 Simulated timing of broods during a 3-year period in eight Austrian rivers, produced by first-generation females of *G. fossarum* born on 1 January 1991 (solid lines) and *G. roeseli* born on 1 March 1991 (dashed lines). Broods are numbered, showing the first and last; some intervening broods are also shown and numbered.

species born on 1 June 1991 in the River March, where midsummer temperatures were on average around 20 °C or above, required less than 150 days to reach maturity and release their first broods. However, due to the strong annual cycle of water temperatures in this river, birth dates had a marked impact on maturation times. For example, *roeseli* born on 1 June 1991 moulted and released the first brood after only 102 days (11 September 1991), but after 300 days (27 June 1992) when born on 1 September 1991. Maturation times were markedly retarded in *roeseli* compared with *fossarum* in the three coldest study rivers, which had mean temperatures below 9.5 °C. Release of the first brood was also later for *roeseli* in the Fischa, where birth dates had the smallest impact on maturation times for both species.

In the Steyr, after release of the first brood the production of further broods during the 3-year simulation period was limited. A maximum of seven

moulted and six broods was calculated for *fossarum* born on 1 March 1991 but only three moulted and two broods for a birth date of 1 December 1991. Even fewer broods were released by *roeseli* in the Steyr, with a maximum of two broods for a female born on 1 March 1991 (Fig. 4) and only one brood (the first) for females with birth dates on or after 1 May 1991. In all of the other study rivers the theoretical maximum of nine adult moulted was achieved within the 3-year period, including one and sometimes two moulted during resting stages in *fossarum*, and up to four in *roeseli* from the Fischa and Voeckla where the number of broods was consequently reduced to five (Table 2). Otherwise, seven or eight broods were released by both species born during 1991, except in the Salzach where *roeseli* born on 1 September 1991 released only five broods. The examples given in Table 2, for females born on 1 March 1991, represent maximum or near-maximum total numbers of offspring released from first-generation females born in 1991.

The simulated maximum number of young in a single brood was slightly larger for *fossarum* than for *roeseli* across the range of rivers investigated. The difference was greatest in the Steyr, where the maximum number of young in a single brood was 15 for *roeseli* compared with 25 in the fifth broods of *fossarum* born in February and March 1991. The largest number of individuals released from single broods (35) occurred in the final broods of *fossarum* born in the Fischa on 1 January 1991 and in the Voeckla on 1 March 1991. The total numbers of offspring born to first-generation females (Total *N* in Table 2) ranged from 127–208 for *fossarum* to 120–169 for *roeseli*, excluding the low numbers from fewer broods in the Steyr.

Theoretical reproductive capacity

The theoretical reproductive capacity (TRC) is the calculated total number of offspring produced by each first-generation female plus the numbers of juveniles born to all her female descendants in a given period of time. Survival rates of eggs or embryos during brood development time were taken into consideration when TRC was calculated. However, survival or mortality rates for other stages in gammarid life cycles are unknown and were not modelled.

The last two columns of Table 2 give the lowest and highest values of TRC for individual *fossarum* and

Table 2 Results from simulations for individual female *G. fossarum* (F) and *G. roeseli* (R) born on 1 March 1991, at natural temperature regimes in eight Austrian rivers

River		First brood		Last brood		All broods Total <i>n</i>	TRC	
		Days/month/year	<i>n</i>	Days/month/year	<i>n</i>		Minimum	Maximum
Steyr	F	561/September/1992	11	1029/December/1993	23 (B6)	120	23	120
	R	808/May/1993	12	912/August/1993	15 (B2)	27	13	28
Salzach	F	402/April/1992	7	819/May/1993	29 (B7)	142	100	2400
	R	461/June/1992	15	897/August/1993	25 (B8)	161	100	800
Erlauf	F	367/March/1992	10	575/September/1992	32 (B8)	188	200	8800
	R	433/May/1992	13	570/September/1992	27 (B7)	157	800	5500
Leitha	F	290/December/1991	11	545/August/1992	27 (B8)	190	700	13700
	R	420/April/1992	16	557/September/1992	27 (B7)	169	1300	7400
Danube	F	198/September/1991	6	525/August/1992	21 (B7)	151	500	12000
	R	196/September/1991	8	529/August/1992	21 (B7)	141	2000	9000
Fischa	F	317/January/1992	14	551/September/1992	33 (B7)	185	800	16000
	R	400/April/1992	21	560/September/1992	26 (B5)	121	1000	4000
March	F	169/August/1991	3	481/June/1992	20 (B8)	127	900	12400
	R	163/August/1991	5	476/June/1992	23 (B8)	120	2900	17300
Voeckla	F	213/September/1991	6	485/June/1992	35 (B8)	208	1800	37600
	R	369/March/1992	25	497/July/1992	29 (B5)	137	5900	8900

Columns under the first and last broods show the number of days, month and year, from birth to release of the brood, and brood number (B2–B8) for the last brood released after nine adult moults, except in the River Steyr; *n* is the number of offspring released from the female's broodpouch. Total *n* is the number of offspring released from all broods produced by first-generation females. Theoretical reproductive capacity (TRC) is the total number of offspring produced by first, second and third generations, as applicable, in the period 1991–93, where the values (to nearest hundred, except Steyr) are for the smallest (minimum) and largest (maximum) numbers released from females born in any month during 1991. Calculations were based on daily water temperatures recorded in the study rivers, assuming that no broods were released during reproductive resting stages in October–November each year for *G. fossarum* and October–February for *G. roeseli*.

roeseli at the temperature regimes of the eight study rivers, resulting from first-generation females born during 1991; TRC was calculated as the total number of offspring produced by the end of 1993. The highest numbers occurred for *fossarum* born in January through to April and for *G. roeseli* born in May and June 1991; minimum values generally occurred in females born during the late summer–autumn months.

In the Steyr a maximum total of 120 juveniles was released in six broods by *fossarum* born on 1 March 1991, but only 28 juveniles were released in two broods by *roeseli* born on 1 April 1991. The much lower fecundity of *roeseli* was partly due to the 5-month reproductive resting stage that was incorporated into the simulation (see Methods). In both species none of the second-generation offspring born at any time in 1991 had matured and reproduced by 31 December 1993.

In contrast, although the Salzach is a relatively cold river, the simulated maximum TRC was 2400 for *fossarum* and 800 for *roeseli*, and second-generation

females contributed to these totals. For both species the minimum and maximum TRC increased greatly with higher mean water temperatures; maxima ranged from 4000 to 17 000 in the Erlauf, Leitha, Danube, Fischa and March (Table 2). These numbers included third-generation offspring born within the 3-year simulation period. In the summer-warm March, TRC for *roeseli* exceeded that for *fossarum* by some 44%, but was only 25% of maximum TRC for *fossarum* in the summer-cool Fischa. The highest calculated values of TRC for *fossarum* were in the winter-warm Voeckla, four times higher than TRC for *roeseli* in that river.

Potential impact of river warming

Simulations indicated that increased levels of temperature between 1 and 3 °C, uniformly applied throughout all months of the year, would increase the viability of both *fossarum* and *roeseli* in the Steyr. For all monthly birth dates in the first year, in both species the life cycles of nine adult moults in first-

generation females were completed within a further 2 years at a temperature rise of 3 °C. At smaller rises of 1 or 2 °C, *roeseli* did not complete the normal life cycle, although there were more adult moults and broods than previously calculated for the temperature regime of 1991–93. A rise of 1 °C resulted in nine adult moults for *fossarum* born between 1 January and 1 April in the first year, but only five moults within a 3-year period for females born on 1 December 1991. Given a rise of 2 °C, *fossarum* born between 1 January and 1 September 1991 completed the life cycle in the Steyr within a further 2 years.

Figs 5 and 6 show the simulated effects of increased temperatures on the total numbers of offspring released from first-generation females born at different times of the year in four rivers, selected to illustrate a range of responses. The largest increases in fecundity were in

the Steyr, where more moults, broods and numbers of released offspring occurred at all rises in temperature between 1 and 3 °C, where they were maximal. Thus, a rise of 3 °C resulted in 144 additional offspring from *fossarum* born in September 1991 and 129 additional offspring from *roeseli* born in March 1991.

In the Salzach, small additional numbers of offspring were produced as a result of the effects of warming in winter and spring, but not in the summer for *fossarum* (Fig. 5), whereas bigger numbers were produced by *roeseli* during the summer months (Fig. 6).

In the homothermous Fischa, increased temperatures in summer slightly favoured reproduction in *roeseli* compared with *fossarum*, but both were adversely affected by raised temperatures in the March, where fewer offspring were produced by females born in the winter and late summer–autumn months.

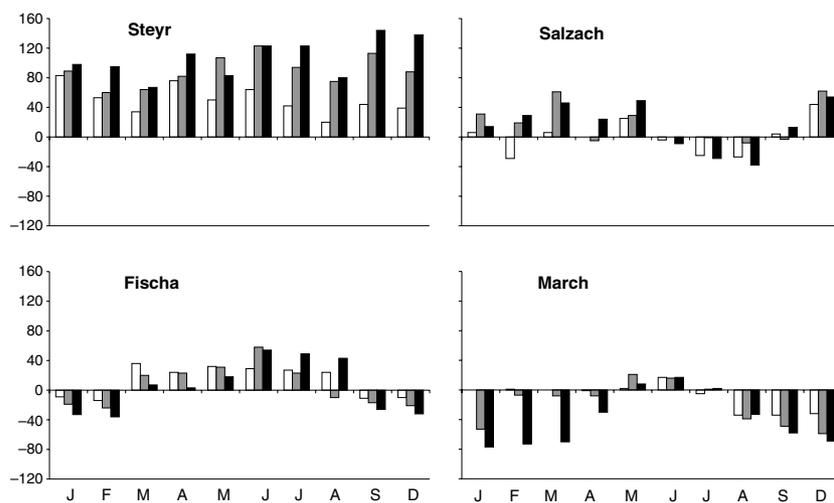


Fig. 5 Simulated effects of raising temperatures in four rivers by 1 °C (white bars), 2 °C (grey bars) and 3 °C (black bars), showing increases and decreases in total numbers of offspring released by first-generation females of *G. fossarum* born in different months during 1991.

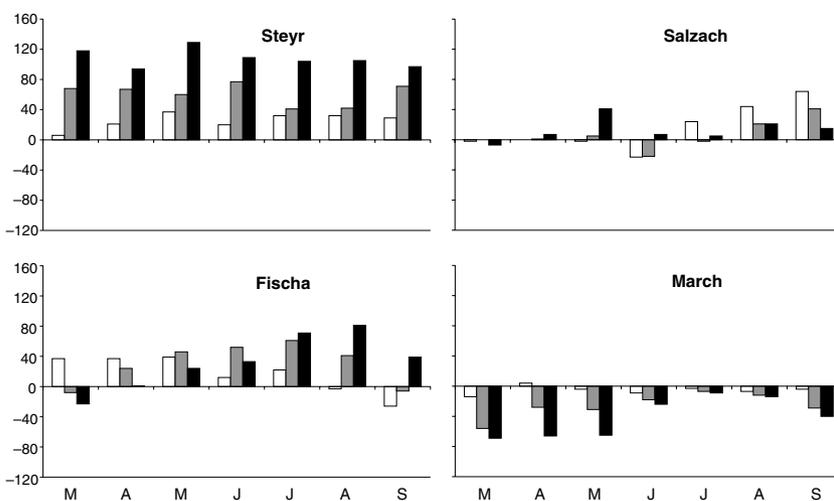


Fig. 6 Simulated effects of raising temperatures in four rivers by 1 °C (white bars), 2 °C (grey bars) and 3 °C (black bars), showing increases and decreases in total numbers of offspring released by first-generation females of *G. roeseli* born in different months during 1991.

The effects of raising river temperatures on TRC were also calculated for a 3-year period. In most of the study rivers, higher values of TRC for both species were obtained because life cycles were faster and more generations were born in a given period, most notably in the Steyr and especially in the Salzach (Fig. 7). However, this did not always occur in the warmest study rivers, where higher temperatures above 20 °C resulted in smaller broods because of increased mortality of the developing eggs. Monthly estimates of TRC for *fossarum* were sometimes less for a rise of 3 °C than for 2 or 1 °C, depending on birth dates in the first year. Similarly, simulations for *roeseli* showed reductions in monthly TRC at higher river temperatures for some birth dates during summer, especially in the Voeckla, although total reproduction increased in females born in the spring; reproduction in *fossarum* also increased greatly at this time (Fig. 7).

Discussion

Our computer simulations assess the relative timing and duration of major life cycle processes that

are important for reproduction in *G. fossarum* and *G. roeseli*, and are influenced by temperature. Without the computer-aided capacity to incorporate natural variations in temperature, on a daily basis, it is extremely difficult to calculate or predict realistic timescales for temperature-dependent rates of growth and reproduction of gammarids that repeatedly reproduce for most of the year and have numerous offspring and overlapping generations. This is especially so when the times required for growth from birth to sexual maturity are relatively long (often occupying 50% or more of the total life span) and occur over periods spanning both winter and summer when temperatures may alter by 20 °C or more.

Different temperature regimes in upland and lowland rivers subtly affect growth and reproduction of gammarids. Higher mean temperatures are generally associated with shorter life spans, faster brood development times, a tendency to produce more broods, and greater potential reproductive capacity in terms of succeeding generations, but the nature of the thermal regime, especially the amplitude of annual variation, exerts an important complicating influence. Moreover, interactions between seasonal

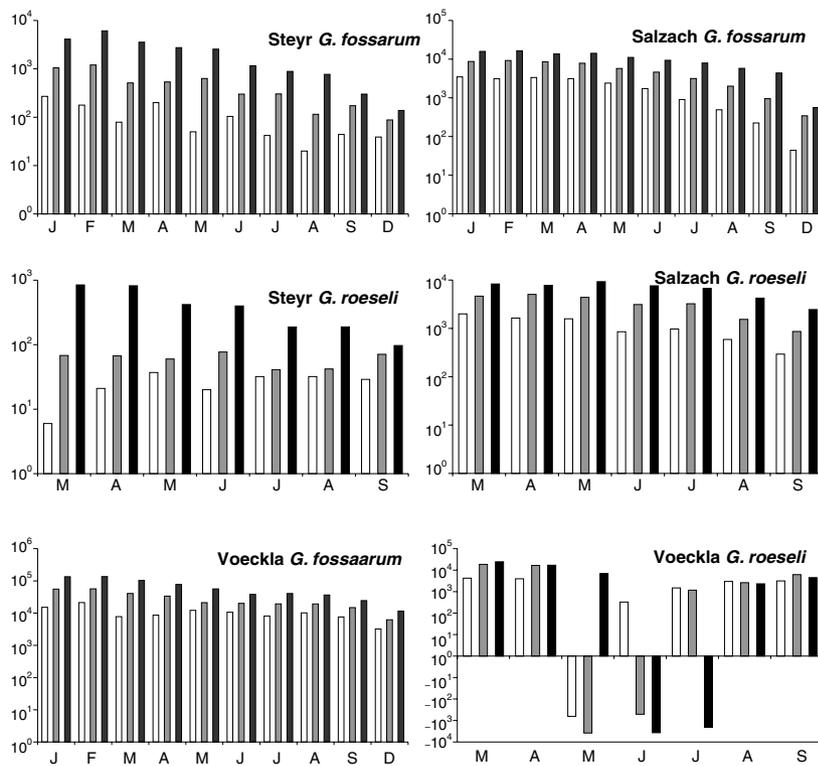


Fig. 7 Simulated effects of raising temperatures in three rivers by 1 °C (white bars), 2 °C (grey bars) and 3 °C (black bars), showing increases and decreases in total numbers of offspring (TRC, log scales) released from first-generation females of *G. fossarum* born in different months during 1991. The results include second- and third-generation offspring produced during 1991–93.

temperature cycles, and the effects of a reproductive resting stage, produced marked differences in the potential reproductive capacity of gammarids with different birth dates during the course of a single year. Similarly, the simulated potential impacts of future river warming varied considerably for females of *fossarum* and *roeseli*, depending on river site, date of birth and fertilisation, and the extent of any rise in water temperature. For Austrian rivers with current mean temperatures in the range *c.* 7–10 °C, future warming could introduce relatively modest changes in gammarid life histories and TRC, whereas the effects would be more positive in cold rivers and negative in warm rivers. The present study underlines the fact that *fossarum* is reproductively more successful than *roeseli* in cooler rivers (Pöckl & Humpesch, 1990; Pöckl, 1993a), but neither species is likely to maintain viable populations in cold rivers that are strongly influenced by snow and ice-melt, such as the Steyr. As mean water temperature increases, *roeseli* increasingly thrives as well as *fossarum*, and may be more successful in the warmest rivers. Nevertheless, there is an upper limit (*c.* 20 °C), beyond which river warming has considerable negative effects on reproductive processes and TRC for *roeseli* as well as for *fossarum*, and our simulations show that overall temperature increases of 2–3 °C in the March and similar summer-warm rivers would potentially reduce the reproductive capacity of both species.

The calculated total numbers of young that successfully hatched and left the maternal broodpouch, during the life span of each female, were usually slightly higher in *fossarum*. This, and earlier maturation times from birth to release of the first brood in *fossarum*, result in larger cumulative numbers of second- and third-generation offspring during a 3-year period. Thus, the values for TRC were higher for *fossarum* in most of the rivers studied here, but not in the March. In this summer-warm river, TRC for *roeseli* exceeded that for *fossarum*, and the former is currently very abundant in the March; relatively high values of TRC for *fossarum* in the Erlauf, Leitha and Fischa also accord with its abundance in these rivers. However, *fossarum* appears to be absent from the March, and simulated estimates of TRC in other rivers do not necessarily indicate actual presence or absence. Numerous other physical–chemical factors, apart from temperature, are known to affect the distribution

of *fossarum* and *roeseli* (Foeckler & Schrimppff, 1985; Schrimppff & Foeckler, 1985; Meijering, 1991; Meyran, 1997).

Until the 1950s, *roeseli* was abundant in the main-stream of the Austrian section of the Danube, but is now rare and largely found immediately downstream from the inflows of lowland summer-warm tributaries where *roeseli* is relatively common. This change in distribution and abundance may partly result from the construction of nine hydroelectric power stations, with barrages and impoundments, along the Austrian Danube. Also, the amphipod fauna of the river is now dominated by immigrants moving upstream from the Pontocaspian area. These include *Dikergammarus villosus* Sowinsky which is considerably larger than *roeseli*, and the smaller *fossarum*, and may have displaced them, perhaps by direct predation as recorded for the lower Rhine (Dick & Platvoet, 2000, 2001).

The predictions of life history and TRC are inevitably based on a number of simplifying assumptions. For example, the reproductive resting period of *fossarum* was defined as lasting from 1 October until 30 November in each year, and that of *roeseli* from 1 October until the end of February. In reality this period is not fixed but varies with temperature, altitude and between stream systems (Pöckl, 1992, 1993a,b, 1995). The assumption of differing resting periods for the two species is likely to be less valid in the Voeckla and the Fischa, where winter water temperatures were in excess of 5 °C, than in rivers that approach freezing. In Table 2 the maximum TRC for *roeseli* in the Fischa and the Voeckla is only a quarter of maximum TRC for *fossarum*. However, if *roeseli* actually had the same resting period as *fossarum*, TRC would be much closer to values typical of the other study rivers. Such an assumption for *roeseli* in these two particular rivers would be justified from published observations, where ovigerous *roeseli* were sampled from the Pielach River in the mild winter of 1986–87 (Pöckl, 1993b). Some eggs developed successfully in the laboratory at a constant temperature of 4 °C but, in contrast to *fossarum*, embryonic development of *roeseli* eggs was not successful at 2 °C (Pöckl & Humpesch, 1990). A precise determination of the duration of the reproductive resting period of gammarids in Austrian rivers and its response to environmental factors would require extensive field-work.

We also assumed that increases in body wet weight follow equation 2 irrespective of the availability of food. Shortages are expected where the only food available is leaf litter and leaf-derived detritus. In small, densely canopied woodland tributaries where higher aquatic plants and algae (except epilithic diatoms) are absent or sparse, seasonal food shortages might occur during which gammarids are not feeding on maximum rations (e.g. Gee, 1988; Pöckl, 1993a, 1995).

Our predictions of TRC are based on an average female specimen for each species. For many life-history variables there is relatively little individual variation in females kept at *constant* experimental temperatures. But growth and fecundity vary considerably within and between populations, ranging from approximately half to twice the average values. This significant variability has been observed at constant temperatures in the laboratory (Pöckl, 1992, 1993a,b, 1995) and might be even greater under naturally fluctuating temperatures in the field (Sarviro, 1983/1984).

In order to calculate actual, rather than theoretical, values for the reproductive capacity of *Gammarus* populations, accurate estimates of survival/mortality rates would be required in rivers with different thermal regimes. Although one of us (MP) has studied the survival of *fossarum* and *roeseli* in long-term laboratory experiments, it has not been possible to develop significant relationships between survival rate and time or temperature. Gammarids are a very important food source for carnivorous invertebrates, fish and other vertebrates (MacNeil, Dick & Elwood, 1997, 1999). In addition, mutual predation, particularly by males upon congeneric reproductive females, may be a powerful force in determining the distribution and abundance of gammarids (Dick, 1996; Dick & Platvoet, 1996). Cannibalism is likely to be a considerable factor in the mortality of *fossarum* and *roeseli*, particularly in the juvenile instars and when moulting. In fact an individual's chances of reaching sexual maturity and entering the breeding population of females must be very low, especially in numerically stable populations where each generation of reproductive females is replaced by similar numbers of the next generation.

Although they are based on several simplifying assumptions, the simulations of TRC over a 3-year period illustrate the relatively high potential reproductive capacity (thousands) of a single female and

her offspring, as a result of a strategy of producing a succession of broods and overlapping generations throughout most months of each year. Thus, in a population containing numerous breeding females, the potential production is theoretically immense (millions). Prolific numbers on this scale indicate that the strategy has evolved to deal with extremely high mortality as a density-dependent feature in populations where the gammarids are relatively abundant. At the same time, and equally important, when circumstances permit there is scope for rapid expansion in population numbers, leading to emigration and occupation of new territory. Migrations upstream as well as down (drift) occur regularly in *fossarum* (Meijering, 1980; Goedmakers, 1981; Statzner & Bittner, 1983) and in other common gammarids, permitting recolonisation of areas in streams denuded by catastrophic events such as floods and droughts. Introductions of gammarids into new geographical regions are frequently characterised by their expansion and spread through waterways, e.g. the post-glacial invasion of mainland Britain by *G. pulex* (Hynes, 1954), and relatively recent introductions of *G. tigrinus* in Britain, Ireland, Germany and the Netherlands (see numerous references in Gledhill *et al.*, 1993 and Dick, 1996).

Finally, with regard to conjectures about future global warming, gammarids (Gammaroidea) evolved long before the Pleistocene (Bousfield, 1983), and modern species of *Gammarus* probably existed by the start of the current Ice Age, with its succession of glacial and interglacial periods. During glaciations, populations of northern species must have contracted and occupied regions south of the ice sheets and probably beyond the influence of very cold ice- and snow-melt waters. Expansion could occur during interglacial warming, equivalent to the current post-glacial phase in the northern hemisphere. However, previous interglacial periods were considerably warmer than now (Jones & Keen, 1993; Lowe & Walker, 1997). At temperatures of 25 °C, individuals and populations of most northern gammarids are increasingly stressed and 30 °C may be fatal. Nevertheless, some could survive in relatively cool streams shaded by woodland and fed by springs and groundwaters, providing refuges until suitable environmental conditions reappeared.

Therefore, we suggest that the high reproductive potential of *fossarum*, *roeseli*, and other common

gammarids, has evolved in response to very high mortality of females (and males) before they reach sexual maturity, coupled with an opportunistic strategy of population expansion following environmental catastrophes that are either short-term (floods, droughts) or long-term (climatic) in extent.

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