



Short-term streambed drying events alter amphipod population structure in a central European stream

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With 4 figures and 2 tables

Abstract: Temporary streams are becoming increasingly common, but ecological responses to streambed drying are poorly characterized in the temperate continental region of central Europe. In addition, global research has focused on community responses to drying, whereas effects on individual populations remain unknown. We explored the population structure of *Gammarus fossarum* (Crustacea: Amphipoda) in a central European temporary stream. Benthic gammarids were sampled on five dates during a flow recession, one date between two drying events (of 10 and 20 days, respectively), and five dates after flow resumed. Additional benthic samples were taken from isolated pools and dry sediments during drying events, and freeze cores were collected to compare the vertical distribution of amphipods during wet and dry phases. Gammarids were measured, adults distinguished from juveniles, adults sexed, and female reproductive state determined. Densities increased during flow recession, potentially reflecting both a decline in submerged habitat availability and seasonal increases in juvenile abundance. Persistence within dry benthic sediments was minimal, whereas pools and saturated subsurface sediments supported high population densities. Juveniles comprised 80% of the subsurface population, suggesting that their ability to inhabit small interstices promotes persistence within the dry reach. Juveniles also comprised 92% of pool inhabitants, despite their potential exposure to predation. Adults dominated after flow resumed, and population structure was altered post-drying by the loss of spring-recruited juveniles and reproductive females. Our results suggest that streambed drying may have longer-term effects than typically characterized by community-level studies. We recommend management actions that support populations of ecologically important species as they adapt to changing flow regimes.

Keywords: drought; hyporheic zone; intermittent rivers and ephemeral streams; population dynamics; recolonization; refuge; refugium; reproductive diapause; river drying

Introduction

Temporary streams, also known as intermittent rivers and ephemeral streams, are those in which water sometimes stops flowing, and in many cases, surface water is lost to leave sediments partly or completely

dry (Datry et al. 2017; Stubbington et al. 2017). Such streams dominate arid zone networks, are common in regions with cooler, wetter temperate climates (Stubbington et al. 2017), and occur in the continental zone of central Europe. Due to increasing drought and heat-wave events (Brázdil et al. 2009; Ledger & Milner

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2015), water resource pressures and land use change, the spatial and temporal extent of drying is increasing in such streams in central Europe and other global regions (Fiala et al. 2010; Laaha et al. 2017; Pyne & Poff 2017). However, whereas the effects of drying on aquatic invertebrate communities have been characterized in temporary streams in central Europe (Pastuchová 2006; Řezníčková et al. 2007; Řezníčková et al. 2010; Řezníčková et al. 2013), population-level impacts of drying remain poorly known here and across regions (Lake 2003).

Instream habitat diversity and availability change as discharge declines in a temporary stream (Boulton 2003). Depending on channel shape, flow recession can reduce the submerged habitat area, and as the water table falls an increasing channel area dries, and surface water may become restricted to persistent or temporary isolated pools (Lake 2003). Water quality may be altered, including temperature increases and reductions in dissolved oxygen availability (Bogan et al. 2017). Depending on the extent to which the water table declines, free water may remain within the benthic and hyporheic sediments after surface water is lost.

The upper reaches of central European streams can be densely populated by *Gammarus fossarum* (Crustacea: Amphipoda), an amphipod that supports ecosystem functioning by transferring energy between trophic levels, as a predator, prey, and shredder of particulate organic matter (MacNeil et al. 1997). Gammarids have limited desiccation tolerance, surviving for only a few days in moist sediments after free water is lost (Stubbington et al. 2009; Poznańska et al. 2013). However, as water levels decline, gammarids can remain submerged by migrating over benthic sediments ahead of a receding waterline (Poznańska et al. 2013). This concentrates populations within a diminishing submerged habitat area (Stubbington et al. 2011), exposing vulnerable individuals such as juveniles to greater risk of predation, including cannibalism (McGrath et al. 2007). If submerged habitats become restricted to isolated pools, biotic interactions can be intense, changing the structure of both communities and populations (Lake 2003; Bogan & Lytle 2011). In addition, poor water quality may affect the metabolic health and therefore reproductive activity of organisms persisting in pools, although such effects remain uncharacterized.

Gammarids may also migrate vertically into the saturated interstices of benthic and hyporheic sediments, in particular if surface water is lost (Vander Vorste et al. 2016a; Vadher et al. 2017). Vertical migra-

tions vary in response to environmental drivers (Stubbington 2012), with experimental studies noting that coarse- and fine-grained sediments respectively promote and reduce Gammarid movements (Mathers et al. 2014; Vadher et al. 2015; Vadher et al. 2017; Vadher et al. 2018a). Vertical migrations may also vary within an individual population: during flowing phases, juveniles may dominate subsurface populations due to the risk of cannibalism by larger adults in the surface sediments, a response facilitated by their smaller size and thus their relative ease of movement through interstices (McGrath et al. 2007). During dry phases, an influx of refuge-seeking adults may create a more balanced population structure within subsurface sediments (Stubbington et al. 2011), if interstitial pathway dimensions are sufficient to accommodate these larger individuals (Vander Vorste et al. 2016a). As in pools, the effects of lower oxygen concentrations and different trophic resources on the physiology of individuals within the hyporheic zone are poorly understood (Findlay 1995).

After flow resumption, gammarids can rapidly recolonize a previously dry reach from perennial surface and subsurface refuges (Meyer et al. 2004; Řezníčková et al. 2007). Drift and upstream migration can provide most recolonists (Meijering 1977; Meyer et al. 2004), with the ability of gammarids to move both upstream and downstream increasing with body size (Lehmann 1967) and larger males therefore most capable of longitudinal migration (Elliott 2005). Migration from hyporheic back to benthic sediments has also been shown experimentally (Vander Vorste et al. 2016b), although gammarid metabolism may be affected by dry-phase persistence within suboptimal habitats. However, true recovery of population structure remains largely unknown (Lake 2003; Lancaster & Ledger 2015), and may be influenced by the representation of juveniles, adult males and adult females in different recolonist sources.

We characterized changes in *G. fossarum* population structure in response to flow recession, two streambed drying events, and flow resumption. Our first hypothesis (hereafter, H1) was that gammarid population densities would change over time, in relation to hydrological variables, and between pre-drying and post-drying phases, and would: (i) increase during flow recession in response to submerged habitat contraction, peaking in isolated pools; (ii) be low in benthic sediments during dry phases, but be higher in subsurface sediments during dry phases compared to wet phases; and (iii) increase after flow resumption.

Our second hypothesis (H2) was that differential survival of different population groups (males, reproductive and non-reproductive females, and juveniles) would alter gammarid population structure over time, in relation to hydrological variables, and between phases, including: (i) a decrease in the proportion of juveniles during flow recession, if the submerged habitat area contracted; (ii) a lower proportion of juveniles in the subsurface sediments during dry phases, if substrate characteristics allowed adults to move into interstices; (iii) a lower proportion of females after flow resumption, due to faster recolonization by males.

Methods

Study site

The Gránický stream (length 13 km, catchment area 20 km², annual discharge ca 7.6 dm³ s⁻¹) is a third-order tributary of the Dyje river in the Podyjí National Park in the Czech Republic, 7 km from Czech-Austrian border (Fig. 1; 48° 52.0' N, 16° 01.5' E). The stream arises in an elevated plateau (410 m a.s.l.) dominated by arable farmland, and the middle and lower reaches meander through a broad-leaved forested valley with minimal human impacts. Schistose granites dominate the bedrock. The upper and lower reaches of the Gránický stream are near-perennial and dried in two extremely dry years in the period 2002–2017 (Řiřicová et al. 2004; Laaha et al. 2017). The studied mid-reach (length 1.5 km, 280 m a.s.l.) is temporary due to sediment permeability and a decrease in stream slope from 2.5% to 1.5%, and dried in 12 years between 2002 and 2017. The temporary reach is locally groundwater-fed, allowing isolated pools to persist for 1–3 weeks at the start of a dry phase, although pools are lost in years in which dry phases exceed this duration.

Based on 1961–2000 records, the mean annual air temperature in the study area is 9.4 °C and mean annual precipitation is 484 mm (Tolasz et al. 2007). Although annual precipitation was comparable to the long-term average in the study year (i.e. 490 mm in 2005; Czech Hydrometeorological Institute 2006), only 16% and 43% of the long-term monthly mean rainfall fell in March (4 mm compared to 27 mm) and June (25 mm compared to 57 mm), respectively. Annual mean air temperature was also comparable to the long-term average in 2005 (9.3 °C; Czech Hydrometeorological Institute 2006), but monthly means were 0.5–1.0 °C above average between April and June.

Field sampling strategy

The study was conducted between April and November 2005, which included two dry phases: 10 days (24 June–3 July) during which surface water was lost from a 600 m stretch, and 20 days (25 July–13 August), when >2 km dried. Isolated pools persisted throughout the 10-day dry phase, and some also retained surface water during the second, longer dry phase. Our study period thus encompassed pre-drying, dry and post-drying phases, and allowed the development of distinct gammarid cohorts to be examined. Based on a visual assessment of the water depth and flow velocity, three dominant instream habitat types were identified within a 20-m stretch of the studied reach: riffle (high velocity, low depth), glide (low velocity, high depth) and marginal (low velocity, low depth). Two riffle, two glide, and (due to its limited spatial extent) one marginal habitat area were each identified by a semi-permanent marker.

Environmental conditions

Water depth and flow velocity (measured with a flow meter at 0.4× depth) were recorded within 50×50 cm plots at ≥100 points at 50 cm intervals within a 7.5 m long stretch. These data were used to calculate the proportion of the channel that was submerged on each date, compared to the maximum submerged area, which was recorded on 25 April during the period of highest discharge (hereafter, % submerged habitat area [%SHA]).

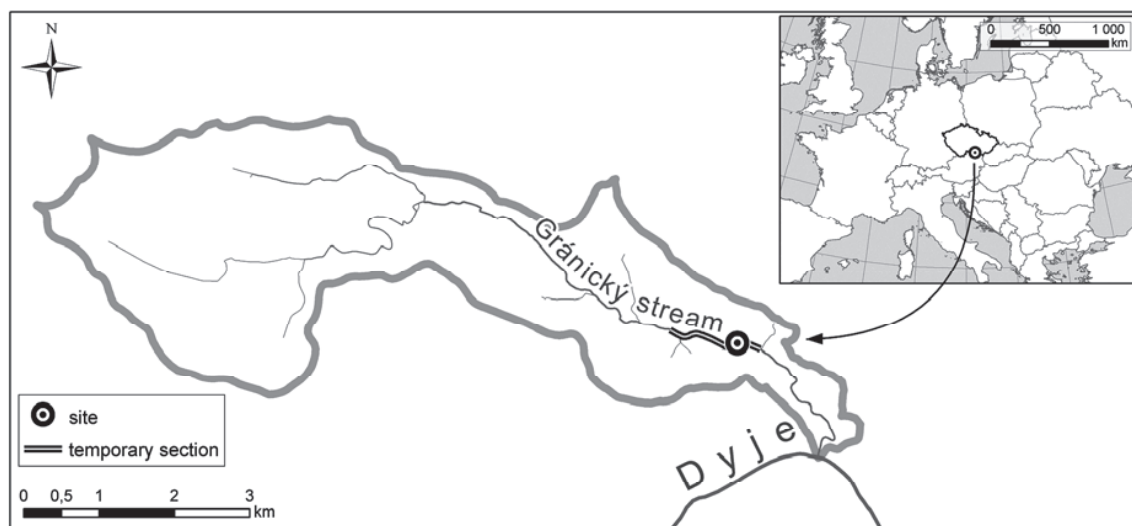


Fig. 1. Map of the study catchment, indicating the position of the study site within the temporary section of Gránický stream, and its location within the Czech Republic and Europe.

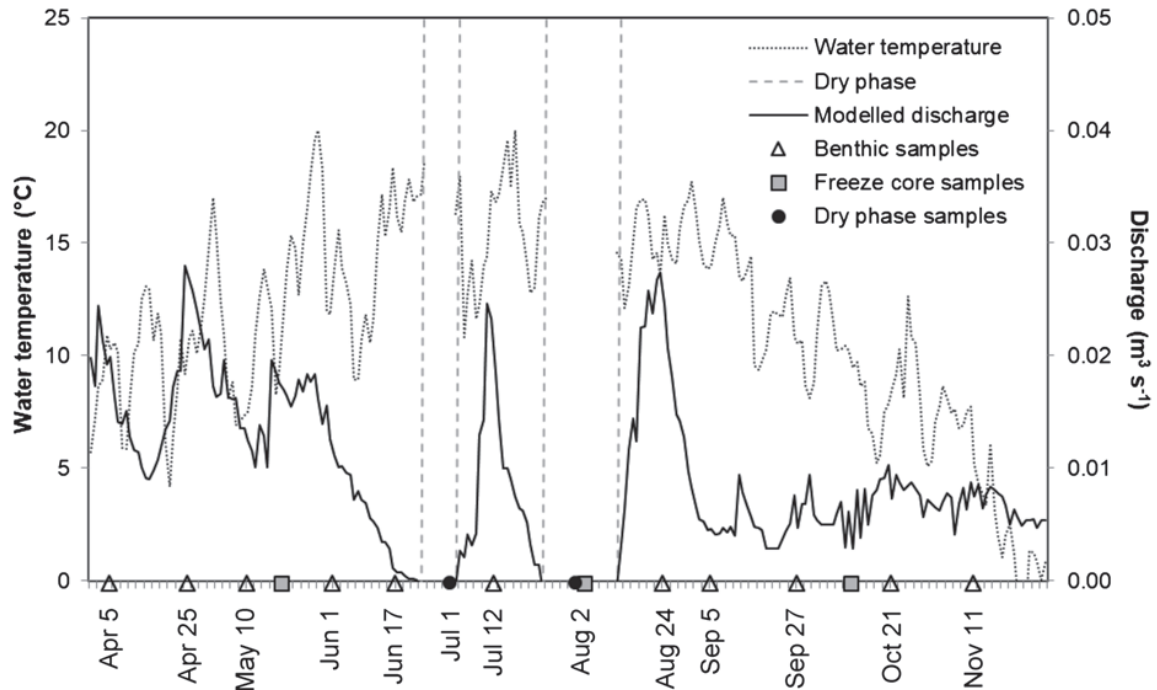


Fig. 2. Water temperature and modelled stream discharge in Gránický stream during the study period (April to November 2005), indicating the timing of flowing and dry phases, and of flowing-phase benthic, freeze-core and dry-phase sample collection.

Discharge was calculated on each sampling date based on flow velocity (at $0.4\times$ and $0.8\times$ depth) and depth measurements from ≥ 8 points at 0.5 m intervals across the channel wetted width. These data and daily precipitation and mean air temperature data from a hydrometeorological station located 4 km from the study area (Kuchařovice $48^{\circ} 52.8' N$, $16^{\circ} 5.1' E$) were used to model discharge and water temperature for the study period (Fig. 2).

On each sampling date, pH, conductivity ($\mu S\ cm^{-1}$), dissolved oxygen concentration ($mg\ l^{-1}$) and saturation (%) and water temperature ($^{\circ}C$) were measured in situ using a multi-parameter probe (Hach-Lange HQ40d). In each habitat area, water depth and flow velocity (at $0.4\times$ depth) were measured using a flow meter, and substrate composition characterized by estimating the proportion of each inorganic substrate category in the AQEM manual (Hering et al. 2004).

Gammarid sampling

To characterize the gammarid population, one benthic sample was collected in each of the five habitat areas (i.e. two in riffle, two in glide and one in a marginal habitat type) by manually disturbing the benthic sediments within a $0.1\ m^2$ frame, 0.5-mm-mesh sampler for 30 s. Samples were collected on each of 11 dates, including five dates in the period preceding drying (hereafter, *pre-drying*), one date during a short flow resumption between two dry phases (hereafter, *between-dry*), and five dates after continuous flow resumed (hereafter, *post-drying*; Fig. 2). In each habitat area, a benthic sample was taken 10–25 cm upstream or downstream of the marker on successive dates, to allow at least 4 weeks for the recolonization of a previously

sampled area prior to re-sampling (Johnson & Vaughn 1995).

Additional gammarid samples were collected during dry phases. First, on day 9 of the second dry phase (2 August; hereafter, *dry-2*), one benthic sample was collected from each of four isolated pools located within 150 m of the main sampling stretch. Second, on one date during both the first dry phase (1 July, hereafter, *dry-1*) and *dry-2* (2 August), one dry benthic sediment sample was collected in each of the three habitat types, by manually excavating sediments within a $0.1\ m^2$ area to a depth of 10 cm.

Benthic and hyporheic bed sediments and associated invertebrates were collected in each of the three habitat types, 30 m downstream of the main sampling area, using the freeze-core technique of Bretschko & Klemens (1986). Cores were taken on three dates: five weeks pre-drying (19 May), on day 11 of *dry-2* (4 August), and two months after flow resumed (11 October; Fig. 2). Standpipes were driven 70 cm into the bed at least 7 d before each date, to allow gammarids to recolonize prior to sampling. On each sampling date, one core was taken from each habitat type using liquid nitrogen. After 20 min of freezing, cores were extracted using a tripod and winch. Each extracted core was divided in the field into 10-cm horizontal layers. Each layer was submerged in water in a calibrated container to determine its volume, then removed and preserved using 4% formalin.

In the laboratory, each layer was elutriated following Omesová & Helešic (2004) and a sieve stack (mesh sizes [mm]: 5, 0.5, 0.25, 0.1) used to separate invertebrates and substrate. A $\leq 0.5\ l$ sediment subsample from each layer was oven-dried at $105^{\circ}C$, separated using consecutive sieves (mesh sizes [mm]: 63, 31.5, 16, 8, 4, 2, 1, 0.5, 0.25, 0.125, 0.063) and weighed.

Grain sizes with an intermediate (*B*) axis > 6 cm were removed, to eliminate the stochastic effects caused by the irregular distribution of large grains (Weigelhofer & Waringer 2003). Weights for each sediment fraction were used to calculate the 25th, 50th and 75th percentiles of each grain-size category for each layer. Coarse particulate organic matter (CPOM) in the dry subsample from each layer was separated using a 0.5-cm mesh sieve and weighed.

Characterization of the gammarid population

To distinguish adults from juveniles, the length of each gammarid was measured from the base of antenna 1 to the tip of the telson (resolution 1 µm) using a stereomicroscope (Olympus SZX9, magnification 3–182×) and QuickPHOTO MICRO image analysis software (version 2.3, © PROMICRA Ltd., Czech Republic). All specimens ≥ 6.5 mm were sexed, with adults and juveniles defined as those above and below this length, respectively. Sex was determined based on the presence of oostegites in females (Pöckl 1992) and the sex-specific shape of gnathopod 2 (Goedmakers 1972). Reproductive females were defined as those with embryos in the brood pouch. For each benthic sample (including flowing-phase, pool and dry sediment samples), we explored population structure by calculating the densities of each population group, and the relative densities (i.e. proportion) of: females compared to all adults, reproductive females compared to all females, and juveniles compared to all gammarids.

Statistical analyses

In total, 55 flowing-phase benthic samples were included in statistical analyses used to test H1-2. In addition, specific hypotheses were explored using: the four benthic isolated pool samples (H1[i]), the six dry benthic sediment samples (H1[ii]) and the nine freeze cores (H1[iii]; H2[ii]). Pool and dry-sediment data were not statistically analysed due to low replication. Analyses were done in R (R Development Core Team 2015), using the *nlme* package for linear mixed models (LMM; Pinheiro et al. 2018). Data distributions were transformed as necessary to meet assumptions of the analyses, including log transformation of density data.

We first used LMM to test for differences in hydrological response variables (water depth, flow velocity and discharge) among hydrological phases (specified as a fixed factor with three levels: pre-drying, between-dry, post-drying). We then used repeated-measures (RM) ANOVA to identify differences in flowing-phase benthic gammarid response variables (i.e. H1: total, male, female and juvenile density; H2: female, reproductive female and juvenile proportion) between dates. To test whether flowing-phase benthic gammarid populations responded to hydrological changes and/or differed among phases (H1), we constructed separate LMM for each response variable. We used stepwise selection based on the Akaike Information Criterion (AIC) to select the best set of explanatory variables (depth, velocity, discharge and hydrological phase) for each response variable using the *stepAIC* function in the *MASS* package (Venables & Ripley 2002). Non-significant variables were removed from the best model if the subsequent model had a $\Delta AIC < 2$ from the best model. We also tested if total, male, female and juvenile gammarid densities (H1[i]) and the proportion of juveniles (H2[i]) varied with %SHA during the pre-drying phase (i.e. 5 dates, $n = 25$) by building separate LMM for

each response variable, with %SHA as the fixed factor. Similarly, we tested if gammarid densities (H1[iii]) and the proportion of females (H2[iii]) changed during the post-drying phase (5 dates, $n = 25$) using LMM with time since flow resumption (i.e. the number of days since the end of dry-2) as the fixed factor. Date was included as a random factor in each LMM model to account for temporal auto-correlation.

One-way ANOVAs using freeze-core densities standardized to core volume were used to compare total and juvenile densities (H1[ii]) and body length (H2[ii]) between wet and dry phases and among the three cores (pre-drying [wet], dry-2 [dry], post-drying [wet]). Spearman rank correlation coefficients (r_s) were calculated to examine relationships between sediment characteristics (depth of layer; 25th, 50th and 75th percentiles of each grain size category; proportion of each grain size category; proportion of CPOM) and population characteristics (total and juvenile densities, and body length mean, maximum and standard deviation). Males and females were excluded from analyses due to low densities.

Results

Environmental conditions

Modelled discharge varied between 1–28 dm³ s⁻¹, interrupted by dry-1 and dry-2 (Fig. 2, Table 1). Heavy rain caused the 21-day flow resumption between these dry phases and re-established flow after dry-2. Compared to the maximum recorded on 25 April (100%), %SHA varied between 54 % and 97% on other dates, declining gradually from 25 April to 54 % on 17 June, 7 days before dry-1 (Table 1). Although velocity was particularly high on the between-dry date (Table 1), such flow peaks are insufficient to mobilize sediments (P. Pařil, unpublished observations) and all hydrological variables were comparable among phases (LMM, all $p > 0.5$). Chemical characteristics of flowing-phase water quality did not exceed values from unpolluted streams during the study (European Commission 2015; Table 1). Mean water temperature was 10.9 ± 0.30 °C and the maximum daily mean was 20.8 °C (Fig. 2). In isolated pools, minimum dissolved oxygen concentrations were 1.8 mg l⁻¹, water temperature peaked at 16.2 °C, and conductivity was always > 1000 µS cm⁻¹ (Table 1).

Hypothesis 1: response of gammarid population densities to hydrological changes and drying

Considering the 55 flowing-phase benthic samples, total, juvenile, male and female gammarid population densities all varied among dates (RM ANOVA, all $F < 11.37$, $p < 0.05$; Fig. 3; Table 2; H1). Total, female and juvenile densities were highest on the final pre-drying date, and male densities on the preceding date (Table 2), and densities of all population groups were

Table 1. Hydrological and water chemistry variables in Gránický stream during flowing phases pre-drying, between two dry phases, in isolated pools during a dry phase ($n=4$), and post-drying. Mean \pm 1 SE or mean values.

Timing		Hydrological variables			Water chemistry variables				
Date	Phase	Discharge ($\text{dm}^3 \text{s}^{-1}$)	Submerged habitat area (%)	Velocity at $0.4 \times$ depth (m s^{-1})	Water depth (m)	Conductivity ($\mu\text{S cm}^{-1}$)	Dissolved oxygen (mg l^{-1})	Dissolved oxygen (%)	pH
5 Apr	Pre-drying	19	94	0.10 ± 0.12	0.14 ± 0.10	797	12.1	107	8.0
25 Apr		29	100	0.17 ± 0.13	0.15 ± 0.09	733	9.2	81	8.7
10 May		14	78	0.11 ± 0.16	0.13 ± 0.09	920	11.8	105	7.8
1 Jun	Between-dry	14	75	0.15 ± 0.20	0.12 ± 0.09	835	8.4	80	9.0
17 Jun		1	54	0.06 ± 0.09	0.10 ± 0.09	874	7.1	71	8.4
12 Jul	Dry	25	97	0.26 ± 0.25	0.15 ± 0.10	715	7.9	80	8.4
2 Aug		NA	NA	NA	0.19 ± 0.07	1123 ± 18	5.1 ± 0.9	$21-88$	8.2 ± 0.15
24 Aug	Post-drying	28	94	0.11 ± 0.12	0.13 ± 0.08	803	7.5	78	8.4
5 Sep		4	61	0.04 ± 0.06	0.11 ± 0.09	1090	9.4	90	8.5
27 Sep		6	65	0.07 ± 0.06	0.10 ± 0.07	998	9.4	86	8.1
21 Oct	Mean	10	86	0.06 ± 0.09	0.13 ± 0.08	904	11.8	101	6.0
11 Nov		9	86	0.08 ± 0.08	0.15 ± 0.09	1070	9.8	81	6.5
		14	81	0.11 ± 0.14	0.13 ± 0.08	87	9.5	885	8.0

Table 2. Mean \pm SE *Gammarus fossarum* response variables in flowing-phase benthic sediment samples collected in Gránický stream, pre-drying, between two drying events, and post-drying; values calculated for $n = 5$ samples on each date, except 25 Apr, $n = 3$ for juveniles; 12 Jul, $n = 1$ for reproductive females / females, $n = 3$ for males; 24 Aug, $n = 1$ for all gammarids / juveniles; 5 Sep, $n = 3$ for all gammarids, $n = 1$ for non-reproductive females / females, $n = 2$ for males, $n = 3$ for juveniles; 27 Sep, $n = 3$ for juveniles; 21 Oct, $n = 4$ for juveniles; 11 Nov, $n = 4$ for males / juveniles; NA, $n = 0$.

Date	Phase	Density (individuals 0.1 m^{-2})				Length (mm)			Proportion (as a %)*	
		Total	Juvenile	Female reproductive	Female non-reproductive	Male	Total	Female	Female reproductive	Juvenile
5 Apr	Pre-drying	85 ± 55	27 ± 22	5.6 ± 0.7	27 ± 18	25 ± 15	9.0 ± 0.7	56 ± 5.7	35 ± 9.9	20 ± 5.9
25 Apr		39 ± 26	8.2 ± 5.3	4.8 ± 3.6	7.4 ± 3.4	19 ± 14	9.4 ± 0.6	47 ± 3.2	21 ± 9.5	17 ± 7.2
10 May		97 ± 32	36 ± 6.8	25 ± 13	11 ± 5.3	25 ± 7.3	7.2 ± 0.3	54 ± 4.4	69 ± 3.2	42 ± 4.4
1 Jun		199 ± 51	139 ± 48	25 ± 3.7	15 ± 5.1	20 ± 4.7	5.9 ± 1.0	65 ± 6.8	67 ± 6.3	62 ± 12
17 Jun		149 ± 120	112 ± 23	14 ± 5.4	5.2 ± 0.9	18 ± 6.4	5.3 ± 0.3	53 ± 7.2	69 ± 3.7	76 ± 3.0
12 Jul	Between-dry	3.4 ± 0.9	2.6 ± 0.7	0.2 ± 0.2	NA	0.6 ± 0.2	4.4 ± 0.8	17 ± 17	1 ± 0	78 ± 9.8
24 Aug	Post-drying	1.4 ± 1.4	1.4 ± 1.4	NA	NA	NA	3.4 ± 0	NA	NA	100 ± 0
5 Sep		3.6 ± 1.7	2.6 ± 1.7	NA	0.4 ± 0.4	0.6 ± 0.4	5.7 ± 1.0	25 ± 25	NA	65 ± 24
27 Sep		15 ± 3.4	5.0 ± 3.2	NA	5.2 ± 1.6	5.2 ± 1.7	9.3 ± 0.9	50 ± 11	NA	26 ± 14
21 Oct	Mean	32 ± 11	3.4 ± 1.2	NA	17 ± 6.5	11 ± 4.5	9.6 ± 0.4	60 ± 5.7	NA	15 ± 7.6
11 Nov		9.4 ± 1.9	2.4 ± 1.1	NA	4.4 ± 1.6	2.6 ± 1.0	7.8 ± 1.0	64 ± 10	NA	31 ± 13

* Female = the proportion of females compared to all adults; female reproductive = the proportion of reproductive (egg- or embryo-carrying) females compared to all females; juvenile = the proportion of juveniles compared to all gammarids.

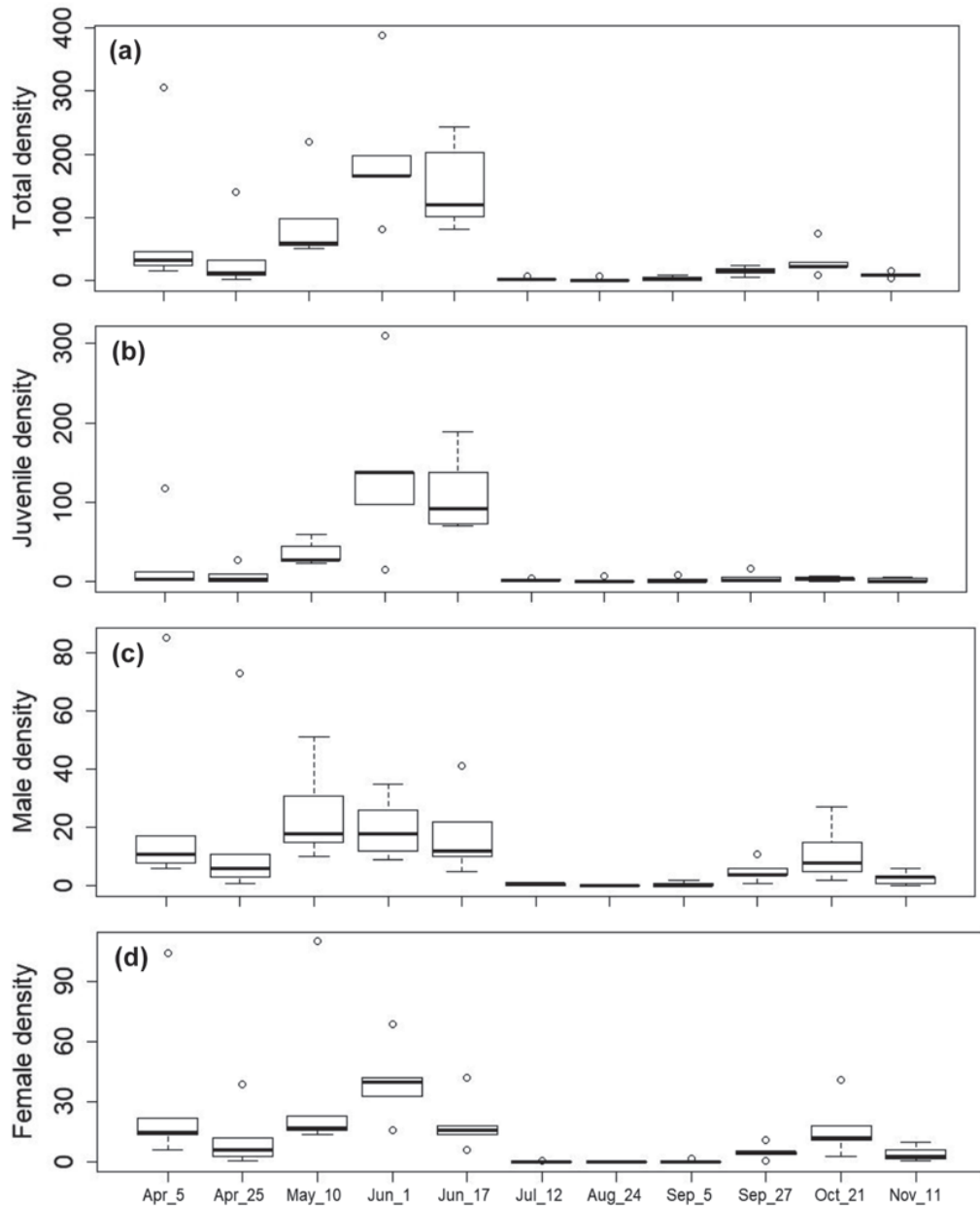


Fig. 3. (a) Total, (b) juvenile, (c) male and (d) female *Gammarus fossarum* densities (0.1 m^2) in samples collected from benthic sediments on five dates pre-drying (Apr 5 to Jun 17), one date between dry phases (Jul 12), and five dates after flow resumed (Aug 24 to Nov 11) in Gránický stream. The box area indicates the first and third quartiles, the central line indicates the median, whiskers represent 95 % confidence intervals, and circles indicate outliers; $n = 5$ for each date.

lowest on the first post-drying date (Table 2; Fig. 3). Total gammarid densities differed among phases and were 10-fold lower post-drying (10.8 ± 2.7 individuals 0.1 m^{-2}) compared to pre-drying (114 ± 20 individuals 0.1 m^{-2} ; LMM, $t = -4.95$, $p < 0.01$), reflecting reduced densities of all population groups (all $p < 0.05$; H1). Total benthic densities declined with increasing discharge (LMM, $t = -2.56$, $p < 0.05$), and juvenile densi-

ties increased with water depth ($t = 2.97$, $p < 0.01$) and decreased with discharge ($t = -3.07$, $p < 0.05$), whereas female and male densities did not vary in response to hydrological variables ($p > 0.05$; H1).

Juvenile gammarid densities increased with declining %SHA (LMM, $t = -3.69$, $p < 0.05$), whereas total, male and female densities did not vary ($p > 0.07$, Table 2; H1[i]).

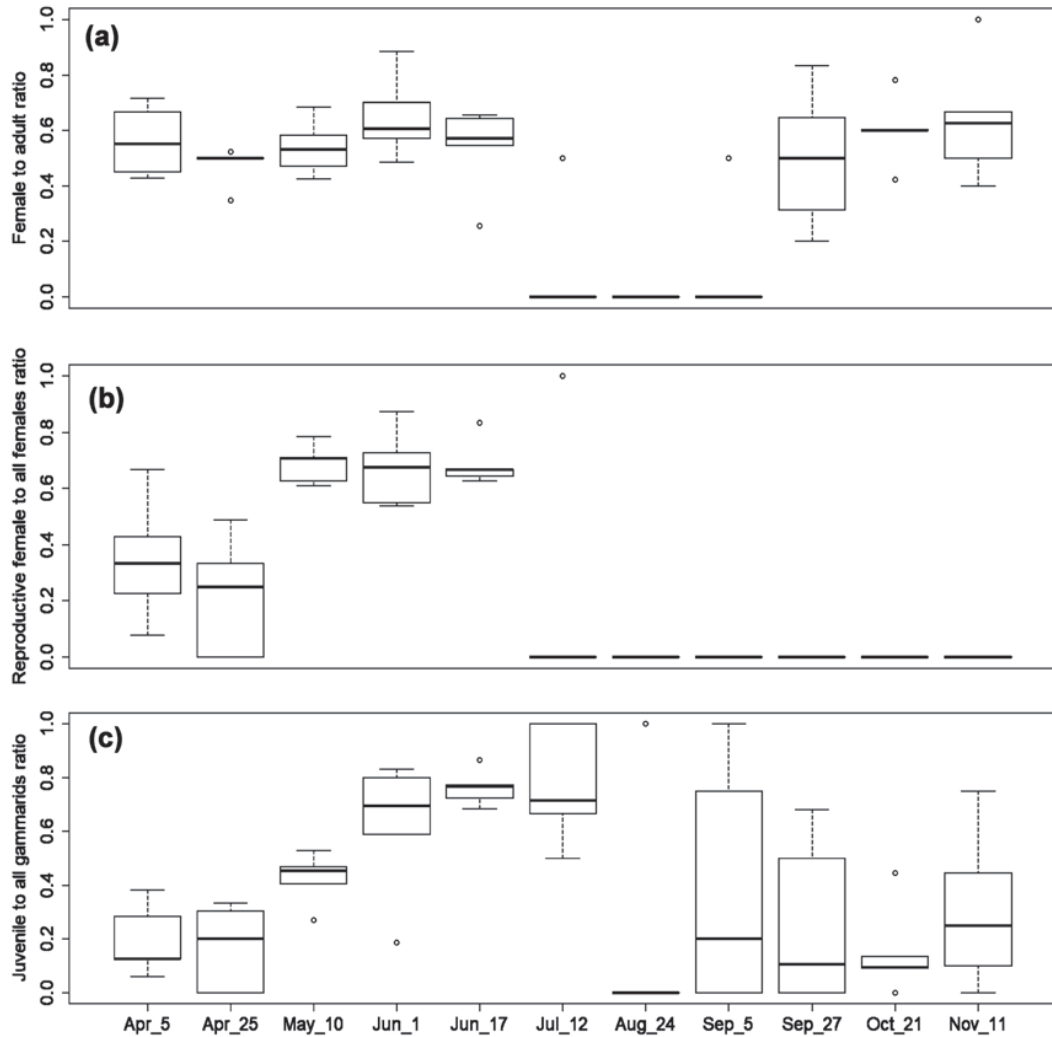


Fig. 4. The proportion of (a) females compared to all adults, (b) reproductive females compared to all females, and (c) juveniles compared to all gammarids in benthic samples collected on five dates pre-drying (Apr 5 to Jun 17), one date between dry phases (Jul 12), and five dates after flow resumed (Aug 24 to Nov 11) in Gránický stream. The box area indicates the first and third quartiles, the central line indicates the median, whiskers represent 95 % confidence intervals, and circles indicate outliers; $n = 5$ for each date, except as stated in the Table 2 title.

Mean total population densities were substantially higher in isolated pools (2723 ± 1306 individuals 0.1 m^{-2}) compared to flowing-phase populations in riffle, glide and marginal habitats ($< 73 \pm 30$ individuals 0.1 m^{-2}), and also greatly exceeded peak densities in these other habitat types (387 individuals 0.1 m^{-2} ; H1[i]; Table 2).

Very few gammarids were observed in dry sediments during dry-1 (4 ± 2 individuals 0.1 m^{-2} ; $n = 3$), and none in samples collected during dry-2 ($n = 3$; H1[ii]). In freeze cores, densities of juveniles (which dominated the population, see below) were higher pre-drying (28 ± 13 individuals per layer) and in particu-

lar during dry-2 (91 ± 71 individuals per layer) compared to post-drying (1.0 ± 0.6 individuals per layer; one-way ANOVA, $p < 0.05$); comparable differences in total densities between pre-drying, dry-2 and post-drying cores were not significant ($p > 0.05$; H1[ii]). Total and juvenile densities (357 and 218 individuals) were almost 10-fold higher in the 0–10 cm layer of the dry-2 pool core than in other layers, with higher water levels observed in this habitat (< 5 cm below the sediment surface) compared to others (approx. 15 cm). Total benthic densities increased from the first to the fourth date after flow resumed, reflecting changes in male and female densities (LMM, all $p < 0.05$),

whereas temporal changes in juvenile densities were not significant ($p > 0.05$; H1[iii]; Table 2).

Hypothesis 2: the response of gammarid population structure to hydrological changes

Considering all gammarids in the 55 benthic samples, the proportion of juveniles (compared to all gammarids), females (compared to all adults) and reproductive females (compared to all females) all differed among dates (RM ANOVA, all $F > 4.11$, all $p < 0.001$; Fig. 4; Table 2; H2). The proportion of juveniles increased with depth (LMM, $t = 2.49$, $p < 0.05$) and decreased with increasing discharge ($t = -3.00$, $p < 0.05$); neither the proportion of females nor of reproductive female responded to any hydrological variable (all $p > 0.08$).

The proportion of juveniles was higher during the pre-drying phase compared to post-drying (LMM, $t = -2.40$, $p < 0.05$; Table 2; H2), and increased from pre-drying dates 2 to 5 in relation to decreasing %SHA ($t = -6.48$, $p < 0.01$; H2[i]). Juveniles dominated the population during the between-dry phase (LMM, $t = 2.80$, $p < 0.05$; Fig. 4c; Table 2) and in isolated pools, where they accounted for 92% of all gammarids, with females and males comprising the remaining 6% and 2%, respectively. The proportion of females compared to all adults did not differ between pre-drying and post-drying phases (LMM, $p > 0.05$) but increased with the time since flow resumption (LMM: $t = 4.79$, $p < 0.05$; Fig. 4a; Table 2; H2[iii]). The proportion of reproductive females compared to all females was higher pre-drying than post-drying (LMM, $t = -6.40$, $p < 0.001$): only one (reproductive) female was sampled during the between-dry phase, and of 135 females sampled across the five post-drying dates, none were reproductive (Table 2; Fig. 4b; H2).

Substrate composition varied among freeze cores and with depth into the bed. Cores from the glide and marginal habitats had an organic-rich surface layer. The 0–20 cm layers comprised larger gravel particles (mean grain size 60 mm) in the riffle core, whereas sand and fine gravel (35 mm) dominated the run core, and marginal core sediments spanned these size classes (50 mm declining to 20 mm). A low-permeability clay layer occurred at a depth of approx. 30–40 cm in the pool and riffle cores, below which mean grain size was lower in the glide core (10 mm) than in other cores (40 mm). Considering densities standardized to core volume, juveniles accounted for 61% of 131, 80% of 429, and 56% of 13 gammarids recorded pre-drying, during dry-2, and post-drying, respectively. Body length was comparable in freeze cores taken pre-dry-

ing (4.5 ± 2.0 mm), during dry-2 (5.2 ± 1.9 mm), and post-drying (11 ± 4.3 mm; one-way ANOVA, $p > 0.05$; H2[ii]). Total gammarid densities ($r_s = -0.64$, $p < 0.05$) and maximum body length ($r_s = -0.47$, $p < 0.05$) decreased with depth; no other significant relationships were observed between gammarid response variables and sediment characteristics (H2[ii]).

Discussion

Our examination of the population structure of the ecologically important amphipod *Gammarus fossarum*, including measurement and sexing of 5967 individuals, provides new insight into population-level responses to drying in central European streams, complementing recent community-level studies (Pastuchová 2006; Řezníčková et al. 2007; Řezníčková et al. 2010; Řezníčková et al. 2013). Our results show that short-term drying events severely reduce amphipod population densities, with the loss of juveniles and absence of reproductive females in the recolonizing assemblage potentially affecting long-term population integrity. By encompassing populations across habitats including isolated pools, dry benthic sediments and saturated hyporheic sediments, our results enable exploration of how refuge use differs between adult and juvenile members of a population.

Response of gammarid population densities to hydrological changes and drying

Our first hypothesis, that gammarid population densities would vary over time in relation to hydrological variability, was generally supported by our data. Contraction of the submerged habitat area, which H1(i) inferred as driving increasing benthic densities, did occur before the first dry phase (dry-1). Juvenile gammarid densities increased as habitat availability declined, which apparently supported H1(i) but is also likely to reflect seasonal increases in juvenile abundance. However, flowing-phase densities of all population groups peaked at 75% SHA on the fourth date, not at 54% SHA on the fifth and final pre-drying date. A notable decline in discharge and velocity occurred between these dates, which (along with intensifying biotic interactions) may have initiated voluntary drift, facilitating entrance into downstream perennial refuges (Meijering 1977; Elliott 2002; Vander Vorste et al. 2016a). Although males may be particularly common in the drift (MacNeil et al. 2003), our data suggest that all gammarids exhibit this behaviour, including females, with benthic densities of females declining by 52% as

discharge fell between dates 4 (200 individuals) and 5 (96 individuals). In addition, gammarids are positively rheotactic (Hultin 1971) and our counts of gammarid movements, recorded on video, document greater upstream migration during late flow recession than during baseflow (P. Pařil, unpublished observations).

Gammarids may also respond to submerged habitat contraction by migrating at the sediment surface ahead of a receding water line (Poznańska et al. 2013). Compared to drift, this may be a lower-risk strategy that promotes use of wet habitats. However, in temporary streams, such migrations can concentrate invertebrates within submerged habitats that contract into isolated pools (Bogan & Lytle 2011; Hill & Milner 2018). Pool inhabitants may be exposed to intense biotic interactions including predation (Berezina 2009) and declining water quality (Boulton 2003, Labaude et al. 2017), and we recorded very low minimum oxygen concentrations. Despite such metabolic stressors, we observed peak densities in isolated pools during dry phases, supporting H1(i). If water levels fall below the substrate surface, as observed in Gránický stream, pool inhabitants may be stranded on drying sediments (Extence 1981; Stubbington et al. 2009), or may migrate vertically into saturated subsurface interstices (Poznańska et al. 2013; Vadher et al. 2017). Gammarid densities were three-fold higher in freeze cores during the dry phase compared to wet phases, and were notably high in the 0–10 cm core layer in an area in which water levels had dropped < 5 cm below the bed. Although we have no statistical support for H1(ii), these observations highlight the importance of perennial subsurface refuges in promoting in-situ survival (Boulton 1989; Bogan et al. 2017).

Gammarids have limited desiccation tolerance and persist for up to a few days after free water is lost (Stubbington et al. 2009; Poznańska et al. 2013). Accordingly, benthic densities declined in Gránický stream by 98–99% after 10-day and 20-day dry phases compared to the final pre-drying date, supporting H1(ii) and previous studies (Meyer et al. 2004; Řezníčková et al. 2007). Such reductions involved all population groups, but juveniles were more persistent than adults, accounting for 13 of 17 and all of seven individuals recorded after dry-1 and dry-2, possibly because their smaller body size enabled their migration into, persistence within, and rapid recolonization from moist subsurface interstices (McGrath et al. 2007). However, we observed very low post-drying densities of all gammarids within freeze cores, suggesting that subsurface sediments may be a graveyard for many individuals (Boulton & Stanley 1995; Young et al. 2011),

especially if the water table drops below the level to which gammarids can move through interstices (Vadher et al. 2015). As such, the hyporheic zone *may* be a major recolonist source, but only where organisms are small enough to enter the interstitial environment and persist there in a viable state until surface flow resumes (Stubbington 2012; Vander Vorste et al. 2016a).

No adult gammarids were recorded on the first date post-drying (11 days after continuous flow resumed), and adults were far less abundant than juveniles in the dry-phase freeze cores, indicating that few adults persisted within the dry reach. However, after flow resumed, increasing gammarid densities reflected adult male and female but not juvenile densities, partially supporting H1(iii). Along with the high proportion of male compared to female adults on post-drying date 2 (discussed below), our observations indicate that male gammarids are important early contributors to population recovery, their ability to recolonize from upstream and downstream perennial surface waters being promoted by their strong swimming ability (Lehmann 1967; Adams & Greenwood 1983; Elliott 2005). In contrast, juvenile abundance remained low post-drying, indicating that drying events may have altered recruitment and therefore population structure, as discussed below.

Response of gammarid population structure to hydrological variability and drying

We hypothesized that differential responses of different gammarid population groups to hydrological drivers would alter population structure, with decreasing juvenile representation as discharge declined reflecting increasing predation of smaller individuals by larger individuals in a contracting submerged habitat area (Bogan & Lytle 2007; Stubbington et al. 2011). In direct contrast to this hypothesized pattern, the proportion of juveniles increased in relation to %SHA (H2[i]). This result, as well as the 92% contribution of juveniles to isolated pool populations, suggests that seasonal reproductive activity and subsequent increases in juvenile abundance offset any increase in predation by both larger conspecifics and other predators, even though vertebrates such as salamanders (which occur in Gránický stream) also discriminate between gammarid prey on the basis of size (Ruff & Maier 2000).

We hypothesized that the proportion of juveniles in subsurface sediments would be lower during the dry phase compared to wet phases due to predation being a size-dependent trigger of vertical migration during wet phases, whereas dry-phase water loss provides size-independent impetus to migrate (H2[ii]). How-

ever, we hypothesized that this dry-phase adult influx would only occur if interstitial pathways accommodated larger individuals, and we explored this hypothesis by relating body size to substrate characteristics. Although mean body size was two-fold higher post-drying (11 mm) compared to pre-drying and during dry-2 (<5.2 mm), very few specimens were recorded post-drying and we found no statistical support for H2(ii). Thus, the smaller size of most sediment inhabitants suggests that interstitial pathway dimensions may have physically restricted vertical movements of larger individuals in Gránický stream (McGrath et al. 2007), regardless of their impetus to migrate. Low replication, low abundance, and the influence of seasonal variability mean that we have insufficient evidence to reject H2(ii); population responses are likely to vary in relation to environmental drivers including sediment characteristics, as previously documented in the field (Descloux et al. 2013) and confirmed by laboratory experiments (Vadher et al. 2015; Vadher et al. 2017; Vadher et al. 2018b).

We hypothesized that the proportion of females compared to all adults would be lower after dry phases (H2[iii]) due to faster male recolonization (Lehmann 1967; Adams & Greenwood 1983, Elliot 2005). Although the proportional representation of females in the population was comparable pre- and post-drying, we found support for our hypothesis: the proportion of females was lowest during the between-dry phase and increased with time after flow resumption, with increasing female densities equalling or exceeding those of male gammarids from the third post-drying date. Our results suggest that, as the initial dominance of larger males with greater dispersal ability declines, females become increasingly important contributors to population resilience after flow resumes. Experimental field studies that characterize recolonization pathways (e.g. Vander Vorste et al. 2016a) are needed to determine whether male and female (and juvenile) resilience is facilitated by comparable or distinct mechanisms.

We did not formulate hypotheses regarding the abundance or proportion of reproductive females, due to the limited evidence available to inform such hypotheses. Our results are nonetheless noteworthy: whereas females with eggs or embryos were more common pre-drying, such females were absent after flow resumed. In perennial streams, *G. fossarum* reproduction continues until late September (Pöckl et al. 2003), whereas exposure to a drying event (which individuals may survive by inhabiting metabolically stressful habitats such as poorly oxygenated pools

and subsurface sediments; Stubbington et al. 2011; Bogan et al. 2017) may have caused early onset of reproductive diapause, as observed in response to other stressors (Ladewig et al. 2006). Previous studies have also suggested that streambed drying, in particular associated with unpredictable drought disturbances, has long-term ecological effects due to reduced recruitment (Boulton & Lake 1992; Resh 1992). An increasing occurrence of drying may gradually reduce population integrity in temporary streams, with impacts rarely characterized due to the community focus of relevant research (Lake 2003).

Conclusions

Most ecological studies of temporary streams explore the effects of drying on communities, leaving population-level effects poorly characterized (Boulton 2003; Lake 2003; Lancaster & Ledger 2015). We show that drying changes population structure, with differential impacts on juveniles and adults skewing populations towards adult dominance. Impacts may be severe if repeated drying events occur, and if high-velocity flow resumptions displace those seeking refuge in subsurface sediments (Stubbington et al. 2016). We observed the absence of reproductive females and severe reduction in juveniles in the first months after flow resumed, highlighting the need to characterize longer-term impacts on population structure. If ecologically important taxa such as gammarids decline in abundance, reduced CPOM processing as well as energy transfer through predation and consumption may alter ecosystem function (Monroy et al. 2016), with changes to food webs potentially spanning multiple trophic levels across aquatic and terrestrial habitats, at spatial scales that reflect the extent of drying (Ledger et al. 2013). Management actions may need to target particular population groups, for example sediment manipulation to enhance the refuge potential of subsurface sediments (Boulton 2007), to promote persistence of juveniles. With changing precipitation patterns interacting with other stressors to increase the extent of intermittence in central Europe (Kadlec 2001; Laaha et al. 2017) and other regions, we call for sensitive management strategies that recognize the value of natural intermittence while supporting populations as they adapt to altered, harsher flow regimes.

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References

- Adams, J., & Greenwood, P. J. (1983). Why are males bigger than females in pre-copula pairs of *Gammarus pulex*? *Behavioral Ecology and Sociobiology*, *13*(4), 239–241. <https://doi.org/10.1007/BF00299670>
- Berezina, N. A. (2009). Interspecific interactions of amphipods *Gammarus lacustris* and *Gmelinoides fasciatus*. *Russian Journal of Ecology*, *40*(2), 81–85. <https://doi.org/10.1134/S1067413609020027>
- Bogan, M. T., & Lytle, D. A. (2007). Seasonal flow variation allows ‘time-sharing’ by disparate aquatic insect communities in montane desert streams. *Freshwater Biology*, *52*(2), 290–304. <https://doi.org/10.1111/j.1365-2427.2006.01691.x>
- Bogan, M. T., & Lytle, D. A. (2011). Severe drought drives novel community trajectories in desert stream pools. *Freshwater Biology*, *56*(10), 2070–2081. <https://doi.org/10.1111/j.1365-2427.2011.02638.x>
- Bogan, M. T., Chester, E. T., Detry, T., Murphy, A. L., Robson, B. J., Ruhli, A., . . . Whitney, J. E. (2017). Resistance, resilience, and community recovery in intermittent rivers and ephemeral streams. In T. Detry, N. Bonada, & A. J. Boulton (Eds.), *Intermittent Rivers and Ephemeral Streams: Ecology and Management* (pp. 349–376). Amsterdam: Elsevier. <https://doi.org/10.1016/B978-0-12-803835-2.00013-9>
- Boulton, A. (1989). Over-summering refuges of aquatic macroinvertebrates in two intermittent streams in central Victoria. *Transactions of the Royal Society of South Australia*, *113*, 23–34.
- Boulton, A. J. (2003). Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. *Freshwater Biology*, *48*(7), 1173–1185. <https://doi.org/10.1046/j.1365-2427.2003.01084.x>
- Boulton, A. J. (2007). Hyporheic rehabilitation in rivers: Restoring vertical connectivity. *Freshwater Biology*, *52*(4), 632–650. <https://doi.org/10.1111/j.1365-2427.2006.01710.x>
- Boulton, A. J., & Lake, P. S. (1992). The ecology of two intermittent streams in Victoria, Australia. III. Temporal changes in faunal composition. *Freshwater Biology*, *27*(1), 123–138. <https://doi.org/10.1111/j.1365-2427.1992.tb00528.x>
- Boulton, A. J., & Stanley, E. H. (1995). Hyporheic processes during flooding and drying in a Sonoran Desert stream. II. Faunal dynamics. *Archiv für Hydrobiologie*, *134*, 27–52.
- Brázdil, R., Chromá, K., Dobrovolný, P., & Tolasz, R. (2009). Climate fluctuations in the Czech Republic during the period 1961–2005. *International Journal of Climatology*, *29*(2), 223–242. <https://doi.org/10.1002/joc.1718>
- Bretschko, G., & Klemens, W. E. (1986). Quantitative methods and aspects in the study of the interstitial fauna of running waters. *Stygologia*, *2*, 299–316.
- Czech Hydrometeorological Institute (2006). *Měsíční přehledy pozorování*. Available at: <http://portal.chmi.cz/historicka-data/pocasi/mesicni-data#> (accessed 1 November 2006).
- Detry, T., Bonada, N., & Boulton, A. J. (2017). General introduction. In T. Detry, N. Bonada, & A. J. Boulton (Eds.), *Intermittent Rivers and Ephemeral Streams: Ecology and Management* (pp. 1–20). Amsterdam: Elsevier. <https://doi.org/10.1016/B978-0-12-803835-2.00001-2>
- Descloux, S., Detry, T., & Marmonier, P. (2013). Benthic and hyporheic invertebrate assemblages along a gradient of increasing streambed colmatation by fine sediment. *Aquatic Sciences*, *75*(4), 493–507. <https://doi.org/10.1007/s00027-013-0295-6>
- Elliott, J. M. (2002). Continuous study of the total drift of freshwater shrimps, *Gammarus pulex*, in a stony stream in the English Lake District. *Freshwater Biology*, *47*(1), 75–86. <https://doi.org/10.1046/j.1365-2427.2002.00782.x>
- Elliott, J. M. (2005). Day-night changes in the spatial distribution and habitat preferences of freshwater shrimps, *Gammarus pulex*, in a stony stream. *Freshwater Biology*, *50*(4), 552–566. <https://doi.org/10.1111/j.1365-2427.2005.01345.x>
- European Commission (2015). Government Regulation No 401/2015 on the indicators and values of permissible surface water and wastewater pollution, details of the permit to discharge wastewater into surface water and sewage systems, and sensitive areas in the Czech Republic. Available at: <http://ec.europa.eu/growth/tools-databases/tris/en/search/?trisation=search.detail&year=2016&num=394> (accessed 1 May 2018).
- Extence, C. (1981). The effect of drought on benthic invertebrate communities in a lowland river. *Hydrobiologia*, *83*(2), 217–224. <https://doi.org/10.1007/BF00008269>
- Fiala, T., Ouarda, T. B., & Hladný, J. (2010). Evolution of low flows in the Czech Republic. *Journal of Hydrology (Amsterdam)*, *393*(3–4), 206–218. <https://doi.org/10.1016/j.jhydrol.2010.08.018>
- Findlay, S. (1995). Importance of surface-subsurface exchange in stream ecosystems: The hyporheic zone. *Limnology and Oceanography*, *40*(1), 159–164. <https://doi.org/10.4319/lo.1995.40.1.0159>
- Goedmakers, A. (1972). *Gammarus fossarum* Koch, 1835: Re-description based on neotype material and notes on its local variation (Crustacea, Amphipoda). *Bijdragen tot de Dierkunde*, *42*, 124–138.
- Hering, D., Moog, O., Sandin, L., & Verdonshot, P. F. (2004). Overview and application of the AQEM assessment system. *Hydrobiologia*, *516*(1–3), 1–20. <https://doi.org/10.1023/B:HYDR.0000025255.70009.a5>
- Hill, M. J., & Milner, V. S. (2018). Ponding in intermittent streams: A refuge for lotic taxa and a habitat for newly colonising taxa? *Science of the Total Environment*, *628*–*629*, 1308–1316. <https://doi.org/10.1016/j.scitotenv.2018.02.162>
- Hultin, L. (1971). Upstream movements of *Gammarus pulex* (Amphipoda) in a south Swedish stream. *Oikos*, *22*(3), 329–347. <https://doi.org/10.2307/3543856>
- Johnson, S., & Vaughn, C. (1995). A hierarchical study of macroinvertebrate recolonization of disturbed patches along a longitudinal gradient in a prairie river. *Freshwater Biology*, *34*(3), 531–540. <https://doi.org/10.1111/j.1365-2427.1995.tb00911.x>
- Kadlec, M. (2001). Statistical review of the historical sum of rains in chosen climatological stations in South Moravia. *International Bioclimatological Workshop, 2001: Weather Extremes as a Limiting Factor of Biometeorological Processes*. Available at: <http://www.cbks.cz/sbornikRackova01/3.html> (accessed 23 May 2018).
- Laaha, G., Gauster, T., Tallaksen, L. M., Vidal, J., Stahl, K., Prudhomme, C., . . . Van Lanen, H. A. (2017). The European 2015 drought from a hydrological perspective. *Hydrology and Earth System Sciences*, *21*(6), 1397–1419. <https://doi.org/10.5194/hess-21-3001-2017>

- Labaude, S., Moret, Y., Cézilly, F., Reuland, C., & Rigaud, T. (2017). Variation in the immune state of *Gammarus pulex* (Crustacea, Amphipoda) according to temperature: Are extreme temperatures a stress? *Developmental and Comparative Immunology*, 76, 25–33. <https://doi.org/10.1016/j.dci.2017.05.013>
- Ladewig, V., Jungmann, D., Köhler, H. R., Schirling, M., Triebkorn, R., & Nagel, R. (2006). Population structure and dynamics of *Gammarus fossarum* (Amphipoda) upstream and downstream from effluents of sewage treatment plants. *Archives of Environmental Contamination and Toxicology*, 50(3), 370–383. <https://doi.org/10.1007/s00244-005-7039-0>
- Lake, P. S. (2003). Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology*, 48(7), 1161–1172. <https://doi.org/10.1046/j.1365-2427.2003.01086.x>
- Lancaster, J., & Ledger, M. E. (2015). Population-level responses of stream macroinvertebrates to drying can be density-independent or density dependent. *Freshwater Biology*, 60(12), 2559–2570. <https://doi.org/10.1111/fwb.12643>
- Ledger, M. E., & Milner, A. M. (2015). Extreme events in running waters. *Freshwater Biology*, 60(12), 2455–2460. <https://doi.org/10.1111/fwb.12673>
- Ledger, M. E., Brown, L. E., Edwards, F. K., Milner, A. M., & Woodward, G. (2013). Drought alters the structure and functioning of complex food webs. *Nature Climate Change*, 3(3), 223–227. <https://doi.org/10.1038/nclimate1684>
- Lehmann, U. (1967). Drift und populationsdynamik von *Gammarus pulex fossarum* Koch. *Zeitschrift für Morphologie und Oekologie der Tiere*, 60(1-3), 227–274. <https://doi.org/10.1007/BF00403495>
- MacNeil, C., Dick, J. T., & Elwood, R. W. (1997). The trophic ecology of freshwater *Gammarus* spp. (Crustacea: Amphipoda): Problems and perspectives concerning the functional feeding group concept. *Biological Reviews of the Cambridge Philosophical Society*, 72(3), 349–364. <https://doi.org/10.1017/S0006323196005038>
- MacNeil, C., Dick, J. T., Hatcher, M. J., & Dunn, A. M. (2003). Differential drift and parasitism in invading and native *Gammarus* spp. (Crustacea: Amphipoda). *Ecography*, 26(4), 467–473. <https://doi.org/10.1034/j.1600-0587.2003.03460.x>
- Mathers, K. L., Millett, J., Robertson, A. L., Stubbington, R., & Wood, P. J. (2014). Faunal response to benthic and hyporheic sedimentation varies with direction of vertical hydrological exchange. *Freshwater Biology*, 59(11), 2278–2289. <https://doi.org/10.1111/fwb.12430>
- McGrath, K. E., Peeters, E. T., Beijer, J. A., & Scheffer, M. (2007). Habitat-mediated cannibalism and microhabitat restriction in the stream invertebrate *Gammarus pulex*. *Hydrobiologia*, 589(1), 155–164. <https://doi.org/10.1007/s10750-007-0731-5>
- Meijering, M. P. (1977). Quantitative relationships between drift and upstream migration of *Gammarus fossarum* Koch, 1835. *Crustaceana, Supplement*, 4, 128–135.
- Meyer, A., Kaschek, N., & Meyer, E. I. (2004). The effect of low flow and stream drying on the distribution and relative abundance of the alien amphipod, *Echinogammarus berilloni* (Catta, 1878) in a karstic stream system (Westphalia, Germany). *Crustaceana*, 77(8), 909–922. <https://doi.org/10.1163/1568540042781702>
- Monroy, S., Menéndez, M., Basaguren, A., Pérez, J., Elosegí, A., & Pozo, J. (2016). Drought and detritivores determine leaf litter decomposition in calcareous streams of the Ebro catchment (Spain). *Science of the Total Environment*, 573, 1450–1459. <https://doi.org/10.1016/j.scitotenv.2016.07.209>
- Omesová, M., & Helešic, J. (2004). On the processing of freeze-core samples with notes on the impact of sample size. *Scripta Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis*, 29, 59–66.
- Pastuchová, Z. (2006). Macroinvertebrate assemblages in conditions of low-discharge streams of the Cerová vrchovina highland in Slovakia. *Limnologica*, 36(4), 241–250. <https://doi.org/10.1016/j.limno.2006.07.002>
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team (2018). *nlme: linear and nonlinear mixed effects models. R package version 3.1-131.1*. Available at: <https://CRAN.R-project.org/package=nlme> (accessed 5 May 2018).
- Pöckl, M. (1992). Effects of temperature, age and body size on moulting and growth in the freshwater amphipods *Gammarus fossarum* and *G. roeseli*. *Freshwater Biology*, 27(2), 211–225. <https://doi.org/10.1111/j.1365-2427.1992.tb00534.x>
- Pöckl, M., Webb, B. W., & Sutcliffe, D. W. (2003). Life history and reproductive capacity of *Gammarus fossarum* and *G. roeseli* (Crustacea: Amphipoda) under naturally fluctuating water temperatures: A simulation study. *Freshwater Biology*, 48(1), 53–66. <https://doi.org/10.1046/j.1365-2427.2003.00967.x>
- Poznańska, M., Kakareko, T., Krzyżyński, M., & Kobak, J. (2013). Effect of substratum drying on the survival and migrations of Ponto-Caspian and native gammarids (Crustacea: Amphipoda). *Hydrobiologia*, 700(1), 47–59. <https://doi.org/10.1007/s10750-012-1218-6>
- Pyne, M. I., & Poff, N. L. (2017). Vulnerability of stream community composition and function to projected thermal warming and hydrologic change across ecoregions in the western United States. *Global Change Biology*, 23(1), 77–93. <https://doi.org/10.1111/gcb.13437>
- R Development Core Team (2015). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available at: <http://www.R-project.org/> (accessed 30 April 2018).
- Resh, V. H. (1992). Year-to-year changes in the age structure of a caddisfly population following loss and recovery of a springbrook habitat. *Ecography*, 15(3), 314–317. <https://doi.org/10.1111/j.1600-0587.1992.tb00041.x>
- Řezníčková, P., Pařil, P., & Zahrádková, S. (2007). The ecological effect of drought on the macroinvertebrate fauna of a small intermittent stream – an example from the Czech Republic. *International Review of Hydrobiology*, 92(4-5), 514–526. <https://doi.org/10.1002/iroh.200610997>
- Řezníčková, P., Soldán, T., Pařil, P., & Zahrádková, S. (2010). Comparison of mayfly (Ephemeroptera) taxocenes of permanent and intermittent Central European small streams via species traits. *Biologia*, 65(4), 720–729. <https://doi.org/10.2478/s11756-010-0067-x>
- Řezníčková, P., Tajmrová, L., Pařil, P., & Zahrádková, S. (2013). Effects of drought on the composition and structure of benthic macroinvertebrate assemblages – a case study. *Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis*, 61(6), 1853–1865. <https://doi.org/10.11118/actaun201361061853>
- Řiřicová, P., Daňhelka, J., Návojevová, H., & Kourková, H. (2004). Drought in the Czech river catchments in 2003 (Sucho v českých povodích v roce 2003). [Vodní Hospodářství]. *Water Management*, 2, 25–29.
- Ruff, H., & Maier, G. (2000). Calcium carbonate deposits reduce predation pressure on *Gammarus fossarum* from sala-

- mander larvae. *Freshwater Biology*, 43(1), 99–105. <https://doi.org/10.1046/j.1365-2427.2000.00527.x>
- Stubbington, R. (2012). The hyporheic zone as an invertebrate refuge: A review of variability in space, time, taxa and behaviour. *Marine and Freshwater Research*, 63(4), 293–311. <https://doi.org/10.1071/MF11196>
- Stubbington, R., Greenwood, A. M., Wood, P. J., Armitage, P. D., Gunn, J., & Robertson, A. L. (2009). The response of perennial and temporary headwater stream invertebrate communities to hydrological extremes. *Hydrobiologia*, 630(1), 299–312. <https://doi.org/10.1007/s10750-009-9823-8>
- Stubbington, R., Wood, P. J., & Reid, I. (2011). Spatial variability in the hyporheic zone refugium of temporary streams. *Aquatic Sciences*, 73(4), 499–511. <https://doi.org/10.1007/s00027-011-0203-x>
- Stubbington, R., Gunn, J., Little, S., Worrall, T. P., & Wood, P. J. (2016). Macroinvertebrate seedbank composition in relation to antecedent duration of drying and multiple wet-dry cycles in a temporary stream. *Freshwater Biology*, 61(8), 1293–1307. <https://doi.org/10.1111/fwb.12770>
- Stubbington, R., England, J., Wood, P. J., & Sefton, C. E. (2017). Temporary streams in temperate zones: Recognizing, monitoring and restoring transitional aquatic-terrestrial ecosystems. *Wiley Interdiscip. Rev.: Water*, 4(4), e1223. <https://doi.org/10.1002/wat2.1223>
- Tolasz, R., Míková, T., Valeriánová, A., & Voženílek, V. (2007). *Climate atlas of the Czech Republic*. Prague: Czech Hydro-meteorological Institute.
- Vadher, A. N., Stubbington, R., & Wood, P. J. (2015). Fine sediment reduces vertical migrations of *Gammarus pulex* (Crustacea: Amphipoda) in response to surface water loss. *Hydrobiologia*, 753(1), 61–71. <https://doi.org/10.1007/s10750-015-2193-5>
- Vadher, A. N., Leigh, C., Millett, J., Stubbington, R., & Wood, P. J. (2017). Vertical movements through subsurface stream sediments by benthic macroinvertebrates during experimental drying are influenced by sediment characteristics and species traits. *Freshwater Biology*, 62(10), 1730–1740. <https://doi.org/10.1111/fwb.12983>
- Vadher, A. N., Millett, J., Stubbington, R., & Wood, P. J. (2018a). Drying duration and stream characteristics influence macroinvertebrate survivorship within the sediments of a temporary channel and exposed gravel bars of a connected perennial stream. *Hydrobiologia*, 814(1), 121–132. <https://doi.org/10.1007/s10750-018-3544-9>
- Vadher, A. N., Millett, J., & Wood, P. J. (2018b). Direct observations of the effect of fine sediment deposition on the vertical movement of *Gammarus pulex* (Amphipoda: Gammariidae) during substratum drying. *Hydrobiologia*, 815, 73–82. <https://doi.org/10.1007/s10750-018-3552-9>
- Vander Vorste, R., Malard, F., & Datry, T. (2016a). Is drift the primary process promoting the resilience of river invertebrate communities? A manipulative field experiment in an intermittent alluvial river. *Freshwater Biology*, 61(8), 1276–1292. <https://doi.org/10.1111/fwb.12658>
- Vander Vorste, R., Mermillod-Blondin, F., Hervant, F., Mons, R., Forcellini, M., & Datry, T. (2016b). Increased depth to the water table during river drying decreases the resilience of *Gammarus pulex* and alters ecosystem function. *Ecology*, 9(7), 1177–1186. <https://doi.org/10.1002/eco.1716>
- Venables, W. N., & Ripley, D. B. (2002). *Modern Applied Statistics with S* (4th ed.). New York: Springer. <https://doi.org/10.1007/978-0-387-21706-2>
- Weigelhofer, G., & Waringer, J. (2003). Vertical distribution of benthic macroinvertebrates in riffles versus deep runs with differing contents of fine sediments (Weidlingbach, Austria). *International Review of Hydrobiology*, 88(34), 304–313. <https://doi.org/10.1002/iroh.200390027>
- Young, B., Norris, R., & Sheldon, F. (2011). Is the hyporheic zone a refuge for macroinvertebrates in drying perennial streams? *Marine and Freshwater Research*, 62(12), 1373–1382. <https://doi.org/10.1071/MF11060>

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