



Persist or perish: critical life stages determine the sensitivity of invertebrates to disturbances

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Received: 20 March 2019 / Accepted: 18 January 2020
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Abstract

A large proportion of studies assessing the impact of disturbances on the invertebrate community composition focus on a single life stage, assuming that those are an adequate indicator of environmental conditions. The effect of a specific disturbance may, however, depend on the life stage of the exposed organism. Therefore, we focused on the effect of spates on the caddisfly *Agapetus fuscipes* CURTIS (Trichoptera: Glossosomatidae) during different larval stages. A 2 year field study was performed in which we measured the discharge dynamics and population development of *A. fuscipes* in four lowland streams in The Netherlands. A stage-structured population model (i.e. StagePop) was used to test the impact of peak discharge on the different life stages, as larval instars 1–4 were not effectively sampled in the field. Four different mortality rates in response to spates were simulated, including a constant low, a constant high, a decreasing and an increasing impact per larval stage. This way, we were able to show a potential association between spates and population declines, where the stage-population model including decreasing impact by spates with increasing larval life stage most accurately described the population development of the larval instars 5–8. Focusing only on late instars could thus potentially result in underestimation of the effects of spates on this species. In conclusion, determination of responses of critical life stages to specific disturbances may help to identify the causes of the presence and absence of species, and thereby aid more effective management and restoration of degraded aquatic systems.

Keywords *Agapetus fuscipes* · Bioassessment · Discharge · Life cycle · Lowland streams

Introduction

Natural flow variations, including spates and droughts, largely determine the spatial and temporal dynamics of invertebrate populations in running waters, as species have evolved traits that enable them to survive, exploit and even depend on these flow regimes (Resh et al. 1988; Poff et al. 1997; Lytle and Poff 2004). Disturbances outside the predictable flow regime to which stream organisms were originally

adapted can, however, reduce population densities, and these adverse effects increase with the frequency, intensity and severity of the disturbance (Poff 1992; Lytle and Poff 2004). A specific disturbance may, however, lead to very different ecological responses depending on the (ontogenetic) life stage of the exposed organism, i.e. eggs, different larval stages, pupae and adults each have different sensitivities (Lancaster and Downes 2010). This was shown for chemical pollution to which early instars of different insect species were commonly more sensitive than later larval stages (e.g. McCahon and Pascoe 1988; Stuijzand et al. 2000; Pineda et al. 2012). For hydrological disturbance it has been postulated that invertebrate responses depend on the timing of the event relative to the life history of the constituent invertebrate species (Boulton 2003; Lytle and Poff 2004; Nijboer 2004). Hence, the timing of harmful events in relation to the critical periods in the life cycle of the exposed species may be important in determining changes in the population structure after a disturbance (Lancaster and Downes 2010; Miller et al. 2012; Wesner 2019).

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00027-020-0698-0>) contains supplementary material, which is available to authorized users.

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Studies assessing the impact of disturbances on invertebrate population dynamics that take the organism's entire life cycle into consideration are, however, rare (but see Kohler and Hoiland 2001; Elliott 2006; Elliott 2013; Pandori and Sorte 2018). Most studies focus on a single life stage, generally late instars or aquatic adults (Lancaster and Downes 2010). This is partly due to the practical limitations involved in the sampling of early instars, since the mesh size of sample nets is commonly too large to retain these small individuals (Cummins and Wilzbach 1988). Alternatively, stage-structured population models (e.g. StagePop) may be used to simulate the impact of a disturbance on life stages that are difficult to sample in the field (Kettle and Nutter 2015). Hereby, the un-impacted population dynamics are modelled by using previously required information on reproduction, natural death rates and stage durations. Different scenarios can then be simulated in which the environmental variables or disturbances have a different effect on the death rates during each life stage, subsequently affecting the population dynamics during later stages (Kettle and Nutter 2015). Such stage-structured population models have previously been used to evaluate the effectiveness of pest control during different life stages of an invasive culicid mosquito species (Wieser et al. 2019). Stage-structured population models were further successfully applied to assess the effects of invasive species and drought on crayfish population dynamics during different life stages (Yarra and Magoulick 2019). Hence, these stage-population models may be a promising tool to simulate the effect of hydrologic disturbances on invertebrate population dynamics during different life stages, including those life stages that are difficult to collect.

The present study applied this approach to the caddisfly *Agapetus fuscipes* CURTIS (Trichoptera: Glossosomatidae), as there is adequate information available on the population dynamics of *A. fuscipes* in unimpacted upper courses of European streams where the species can locally reach high densities (e.g. Nielsen 1942; Castro 1975; Becker 1990; Sangpradub et al. 1999; Becker 2005). *A. fuscipes* is a case-building species with a univoltine life cycle consisting of an egg stage, eight larval instars, a pupae stage and a terrestrial flying adult (Castro 1975). Several life stages of *A. fuscipes* are generally simultaneously present in the stream (Becker 2005). Some knowledge on the stress responses for different life stages of *A. fuscipes* is already available, showing that unpredictable drops in stream water levels may result in the desiccation and subsequent loss of pupae above the water line (Nielsen 1942; Marchant and Hehir 1999). A laboratory experiment showed that late instar larvae endure more respiratory difficulties than early instar larvae when material is deposited upon them (Majecki et al. 1997). Moreover, terrestrial adults may be affected by disturbance of the riparian vegetation, with attendant impacts on larval population densities (Harrison et al. 2000). The literature is, however,

ambiguous concerning the sensitivity of *A. fuscipes* to spates. Some studies reported that *A. fuscipes* populations were very susceptible to spates (Jones et al. 1977), while others reported that larvae were relatively unaffected (Giller et al. 1991). The discrepancy between these studies may be related to the timing of the peak discharge in relation to its life cycle, as argued above, but this explanation lacks verification.

Therefore, we aimed to gain a better understanding of the effect of spates on the population dynamics of *A. fuscipes* during different larval stages. We hypothesized that first instar larvae are more sensitive to spates than final instar larvae, i.e. high currents may cause dislodgment of first instar larvae as they attach themselves poorly to the gravel (Jones et al. 1977; Nijboer 2004). To test this hypothesis, we performed a 2 year field study in which we measured discharge dynamics and the population development of *A. fuscipes* in four lowland streams in The Netherlands and tested the larval instar specific mortality rates in response to spates using a stage-structured population model. Normally, these four streams have a relatively stable discharge pattern. However, in the first year of the field study several severe spates occurred, providing a 'natural experiment' to evaluate the effect of these spates on the population development of *A. fuscipes* compared to the more stable second year.

Materials and methods

Study area

The field study was performed in two regions in The Netherlands, one region in Zuid-Limburg (region I: 50°54' N; 5°48' E), and one region in the Veluwe (region II: 52°04' N; 5°52' E) (Fig. 1a). In each region, two headwater streams were selected; region I Bunderbosbeek (BU) and Strabekervloedgraaf (ST; Fig. 1b), region II Seelbeek (SE) and Oude beek (OB). The water chemistry differed between the two regions, as the soil in Zuid-Limburg is more calcareous than in the Veluwe, leading to a higher mean pH (BU = 7.2 ± 0.1 and ST = 7.3 ± 0.2 vs SE = 6.9 ± 0.2 and OB = 7.0 ± 0.1), higher mean electrical conductivity (BU = 702 ± 108 and ST = 558 ± 90 vs SE = 342 ± 48 and OB = 193 ± 11 µS/cm) and higher concentration of some micro-ions in the stream water (Supplementary material A, Table S1). In spring and autumn, mean daily water temperatures were similar in the four streams (Supplementary material A, Table S1 and Fig. S1a). In summer, the water temperature was higher in the ST stream than in the other streams, while in winter the water temperature was lower in the ST and SE streams than in the BU and OB streams. In each stream, two

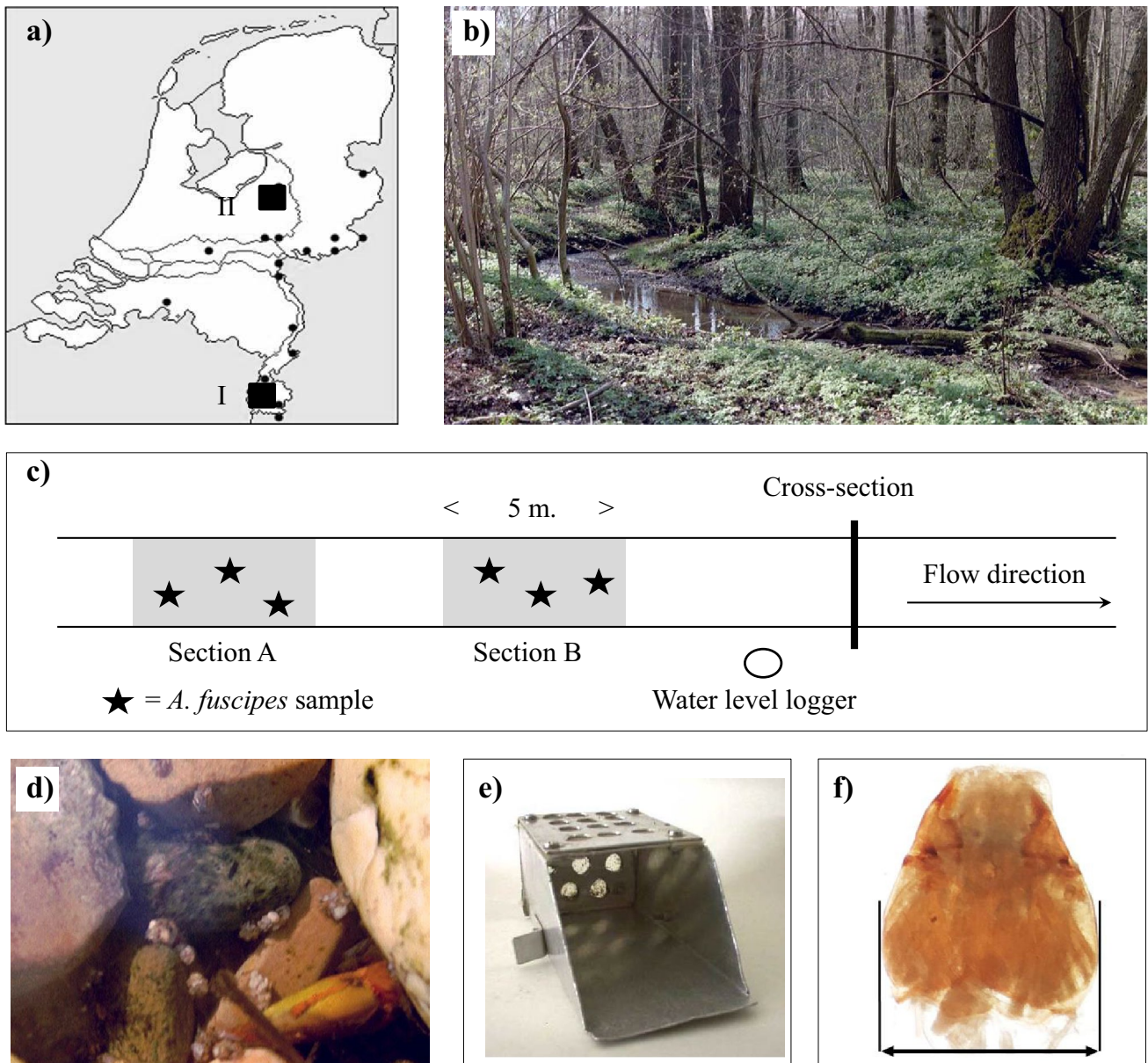


Fig. 1 **a** Occurrence of *A. fuscipes* (dots) and location of study regions (squares) in The Netherlands: I Zuid-Limburg and II Veluwe, **b** picture of the Strabekervloedgraaf (ST stream), **c** schematic over-

view of the field set-up, **d** *A. fuscipes* larvae on gravel bed, **e** shovel used for sampling, **f** measured head capsule width of *A. fuscipes*

sections of 5 m length were selected, which were up to 10 cm deep and up to 2 m wide (Fig. 1c). Coarse gravel was the most frequently observed substrate category in each section, i.e. 59% coverage in the SE stream, 61% in the OB stream, 74% in the BU stream and 83% in the ST stream (Supplementary material A, Fig. S2). Larvae generally inhabit these gravel beds, feeding on biofilms growing on hard substrates (Fig. 1d; Castro 1975; Becker 1990).

Data collection

Discharge dynamics The water level (m) of each stream was measured every 15 min for 2 years from April 2002 until April 2004 with a mini-Troll model ssp-100 (In-Situ inc, Ft. Collins, CO, USA) installed in a monitoring well (Fig. 1c). To be able to translate the water level measurements into discharge, a cross-section profile of the stream was measured every 2 weeks at 10 cm intervals across the channel. Discharge (Q) was calculated in m³/s from the corrected water level and cross-section data using the slope-area method

(Boiten 2000; details in Nijboer et al. 2003). Discharge data were normalized to the median flow (Q_{50} or base flow) to enable comparison of the streams with different flow magnitude (Riis et al. 2008).

Agapetus fuscipes Population density and head capsule width were measured every 2 weeks during the first year. In the second year sampling was continued every 3 months, which was considered sufficient to follow general trends in population dynamics based on the results from the first year. In each 5 m stream section, three random samples were taken from the gravel beds (Fig. 1c; $N=6$ per stream). For each sample, the top gravel layer was collected with a shovel from a surface area of 45 cm^2 and placed into plastic buckets (Fig. 1e). A total area of 270 cm^2 was sampled per stream. This sampling surface was considered sufficient as the density of *A. fuscipes* was very high on these gravel beds, and could reach up to 388 larvae/ 270 cm^2 (25th percentile = 9; median = 64; 75th percentile = 103 larvae/ 270 cm^2). The samples were stored for one night aerated at $5\text{ }^\circ\text{C}$, sieved through a 0.16 mm mesh sieve and sorted. All larvae and pupae of *A. fuscipes* were preserved in 70% ethanol. The head capsule width was measured under $50\times$ magnification with a microscope equipped with a horizontal micrometer scale, to the nearest 0.025 mm (Fig. 1f). The *A. fuscipes* larvae were assigned to eight larval instars, based on the head width classes defined by Castro (1975). Based on the entire sampling collection over 2 years, the number of specimens increased from the first larval instar to the fifth (Fig. 2), suggesting that early instars 1–4 were not collected effectively from the field.

Stage-structured population model

As larval instars 1–4 were not collected effectively from the field, we used a stage-structured population model to analyze the effect of peak discharges on the development of the *A. fuscipes* population density. The natural life cycle of the population was modeled using the delay-differential equation formulation by Nisbet and Gurney (1983). This formulation assumes that once an individual is born it passes through different life stages, unless it dies. The stage durations and background or natural death rates were based on parameters measured previously in unimpacted streams (see “Model parameters”). Discharge peaks were then used as input to the model to alter the mortality rates of each individual in the population based on its life stage and the intensity of the spate. This way we could assess the effect of discharge during all stages, i.e. also those that were not sampled effectively, on the population development during later stages. We simulated four scenarios with different sensitivity (mortality rates) to spates and tested which scenario corresponded best with the measured *A. fuscipes* population density of larval instars 5–8 (see “Model testing”).

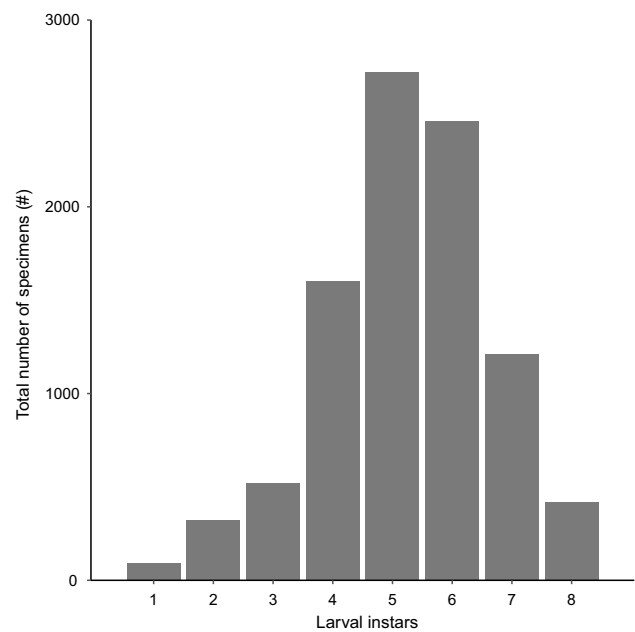


Fig. 2 Number of specimen per larval instar collected during the entire sample collection period of 2 years

Model parameters

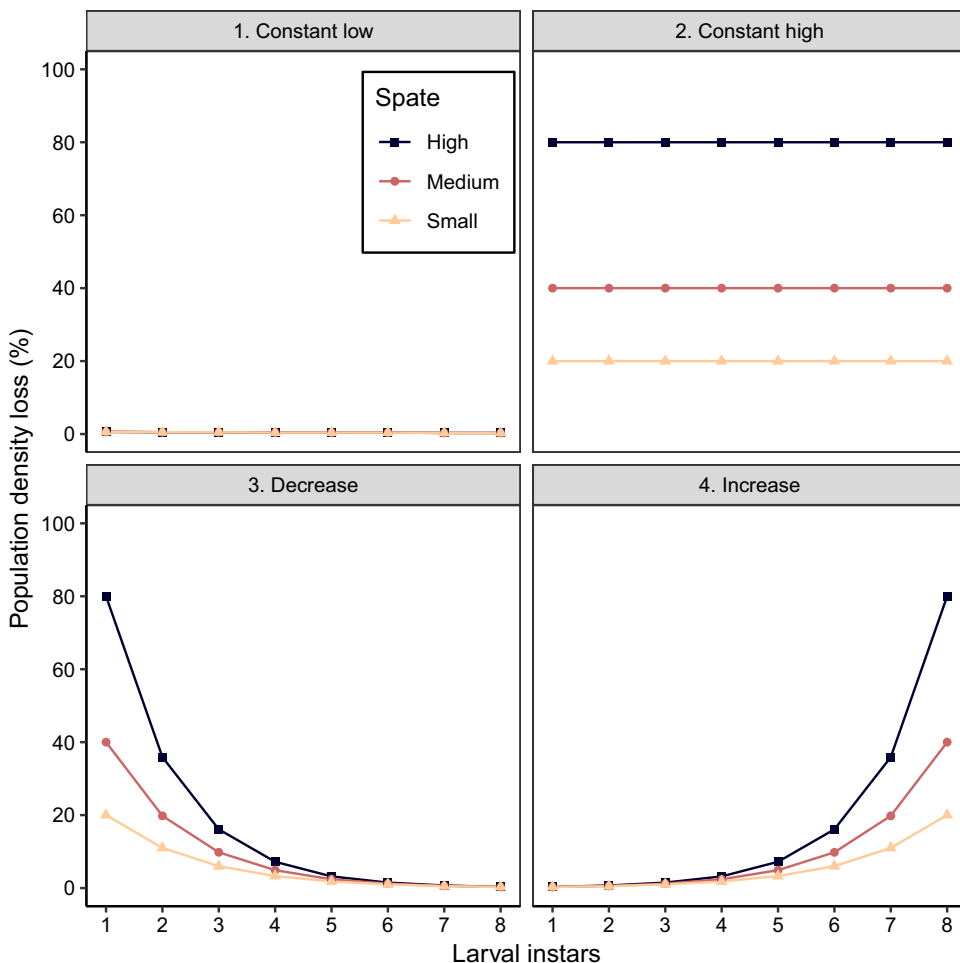
Parameter values were obtained from Castro (1975), who extensively monitored *A. fuscipes* in the Breitenbach, an unimpacted headwater stream in Central Germany with dimensions and temperature regimes similar to our studied streams (Supplementary material A, Fig. S1b). The stage-structured population model comprised the egg stage, the eight larval instars, the pupal and adult stage. The time for one larval instar to develop into the next instar depends on the cohort and water temperature (Castro 1975). After each moult, the larvae leave their old case and build a new one from sand grains (Hanna 1961). The mean durations of these stages over all cohorts were 33, 25, 34, 44, 42, 45, 50, 40, 27, 29, and 4 days, respectively (Castro 1975). The sex-ratio was 2:1 ($\text{♂}:\text{♀}$), with a female laying 200 eggs on average during her 4 day life as an adult, so we simplified the reproduction rate to $200/4 = 50$ eggs per female per day (Castro 1975). Background mortality rates were estimated from the data on population density of larval instars 4–8 of Castro (1975), by dividing the area under the density curve by the duration of each larval instar (Southwood 1978). The other stages were either not sampled or not sampled effectively, so we extrapolated the results assuming a linear trend. This resulted in slightly higher background mortality rates of the early life stages than those of the later life stages, decreasing from 0.016 to 0.006 day^{-1} .

Model testing

The simulation was initiated with the immigration of 1 adult per day over 120 days, as most adults emerge over a 4 month period, resulting in the presence of several developmental stages present at the same time (Becker 2005; Nijboer 2004). For each measurement year the model was run separately, as *A. fuscipes* populations may recover quickly after stress (Nijboer 2004). A ‘spin up’ time was applied to get all stages established, with 394 days for the BU stream, SE stream and OB stream and 424 days for the ST stream to match the respective pupation period in each stream. To determine the effect of spates we selected discharge peaks exceeding thresholds relevant for invertebrate communities in lowland streams, including small spates of 2–4 times the Q_{50} , medium spates of 4–8 times the Q_{50} and high spates of > 8 times the Q_{50} (Verdonschot and van den Hoorn 2010). Mortality rates were set to test four different scenarios (i.e. responses) to spates: (1) constant low, no impact by spates, (2) constant high, all larval stages are highly sensitive to spates, (3) decrease with instar stage, the sensitivity of the larvae to spates decreases with increasing larval stage, and (4) increase with instar stage, the sensitivity of larvae to spates increases with increasing larval stage (corresponding mortality rates for population density loss in each model in Supplementary material B)

larval stages are highly sensitive to spates, (3) decrease with instar stage, the sensitivity of the larvae to spates decreases exponentially with increasing larval stage, and (4) increase with instar stage, the sensitivity of larvae to spates increases exponentially with increasing larval stage (Fig. 3). We assumed a density loss of 80% for high spates, 40% for medium spates, and 20% for small spates (Bond and Downes 2003; Death 2008; Supplementary material B). The root mean square error (RMSE) was then used to test which scenario corresponded best with the measured *A. fuscipes* population density development of larval instars 5–8. The RMSE estimates the standard deviation of the model, so smaller values indicate a better fit. The unit is the same as the unit of the dependent variable, i.e. number of specimen/270 cm². The analysis was performed in R version 3.4.1, using r package ‘StagePop’ to construct the stage-structured population models (Kettle and Nutter 2015), ‘PBSddesolve’ to solve the delay- differential equations (Schnute et al. 2013) and ‘Metrics’ to calculate the RMSE values (Hamner et al. 2018).

Fig. 3 Four potential scenarios for the effects of spates on *A. fuscipes* population density losses per larval instar: 1) constant low, no impact by spates, 2) constant high, all larval stages are highly sensitive to spates, 3) decrease with instar stage, the sensitivity of the larvae to spates decreases with increasing larval stage, and 4) increase with instar stage, the sensitivity of larvae to spates increases with increasing larval stage (corresponding mortality rates for population density loss in each model in Supplementary material B)



Results

Discharge dynamics The base flow (Q_{50}) was higher in the OB stream ($0.014 \text{ m}^3/\text{s}$) than in the other three streams ($0.004 \text{ m}^3/\text{s}$). The flow duration curves showed that in the BU stream more peak discharges occurred in the first measurement year than in the second year (Supplementary material C). All peak discharges took place from May to October 2002 with one high spate (> 8 times the Q_{50}) on 13 July 2002 (Fig. 4a). Discharge peaks occurred during both years in the ST stream, although they were higher in the first year. High spates took place on 13 July, 20 and 21 August, and 3 November 2002 (Fig. 4b). Discharge in the SE stream was rather stable during both years, as only some small spates occurred between April and May 2002 and one in November 2002 (Fig. 4c). In the OB stream, more peak discharges occurred in the first year than in the second year, with one high spate on 27 October 2002 (Fig. 4d).

Agapetus fuscipes Pupae started to appear from the end of March in the ST stream and the end of April in the BU, SE and OB stream (Fig. 4). In all streams, the majority of the individuals had pupated by September. Matching the start of the pupation period of the model to the data on *A. fuscipes* resulted in comparable timing between the model and the data for the larval instars 5–8. In all streams, the population density of larval instars 5–8 was lower in the first measurement year than in the second year, except for the OB stream where the population density was similar during both years.

In the BU stream, a high spate and several smaller spates occurred in the first year when primarily larvae of instar stages 1–3 were present (Fig. 4a). Here, the models including either a constant high impact by spates or a decreasing impact by spates were better able to represent the population development in larval instars 5–8 than the models including either a constant low impact by spates or an increasing impact by spates (Table 1). In the ST stream, spates of various intensities occurred during different life stages (Fig. 4b). The model including a decreasing impact by spates most accurately described the population development in larval instars 5–8 in this stream (Table 1). In the SE stream, several small spates occurred between instar stage 7 to instar stage 1 (Fig. 4c). The model including a constant high impact by spates most accurately described the population development in larval instars 5–8 (Table 1). In the OB stream, the population density of larval instars 5–8 was similar during both years (Fig. 4d). The high spate during instar stages 4–6 did not seem to be associated with a decrease in population density. The model including decreasing impact by spates most accurately described the population development in larval instars 5–8 in this stream (Table 1).

Discussion

For three of the four studied streams the stage-population model including a decreasing impact by spates with larval life stage most accurately described the *A. fuscipes* population development of larval instars 5–8, supporting our hypothesis. It must be stressed that the study was based on a ‘natural experiment’ where several high spates occurred during early stages, while there was only one data point for a high spate during later periods in the life cycle. In the fourth stream, the population density of larval instars 5–8 was most accurately described by the model including constant high impact by spates. In that stream only several small spates occurred between instar stage 7 to instar stage 1 in the first year. The lowered population density of larval instars 5–8 in that year may not have been directly related to the flow, but instead to the large amount of deposited sand, silt and detritus on the gravel beds during this period (extra observations in Supplementary material A, Figure S3). *A. fuscipes* larvae may endure respiratory difficulties when material is deposited upon them, in particular during later stages (Majecki et al. 1997). The effects of flow and sediment transport are, however, difficult to separate as both factors interact (Hynes 1970). Controlled experiments are needed to understand the mechanistic effects of flow and sediment transport on invertebrate species during a spate (e.g. Bond and Downes 2003; Gibbins et al. 2007), but to our knowledge such experiments have not been combined with testing for the effect on specific life stages.

Comparable to our study, Elliott (2006) assessed the effects of a severe spate on different life stages of four Elmids beetle species in a ‘natural experiment’. The effects of the spate were negligible for the larvae as they were buried in the gravel, which served as a refuge from the spate. In contrast, all adult densities were negatively affected by the spate, but the magnitude varied between species, presumably related to species specific habitat requirements (Elliott 2006). The same spate had limited effect on a Baetid mayfly, as the specimens present during the spate were in larval stages 2–3, and probably small enough to burrow between small stones in the substratum to avoid effects of the spate (Elliott 2013). In agreement with these studies, Sagnes et al. (2008) observed that the aquatic insect larvae can make use of different hydraulic habitats while growing, i.e. dependent on the species they may prefer higher or lower shear velocity conditions with increasing larval stage. Beside the timing of spates during the invertebrate life cycle, Lancaster (1992) concluded that the time of day at which a disturbance takes place should be taken into account when interpreting the effect of peak discharges on invertebrates, as the density of *Baetis* nymphs in her study was reduced significantly by the spate created after sunset, but not at dawn or mid-afternoon.

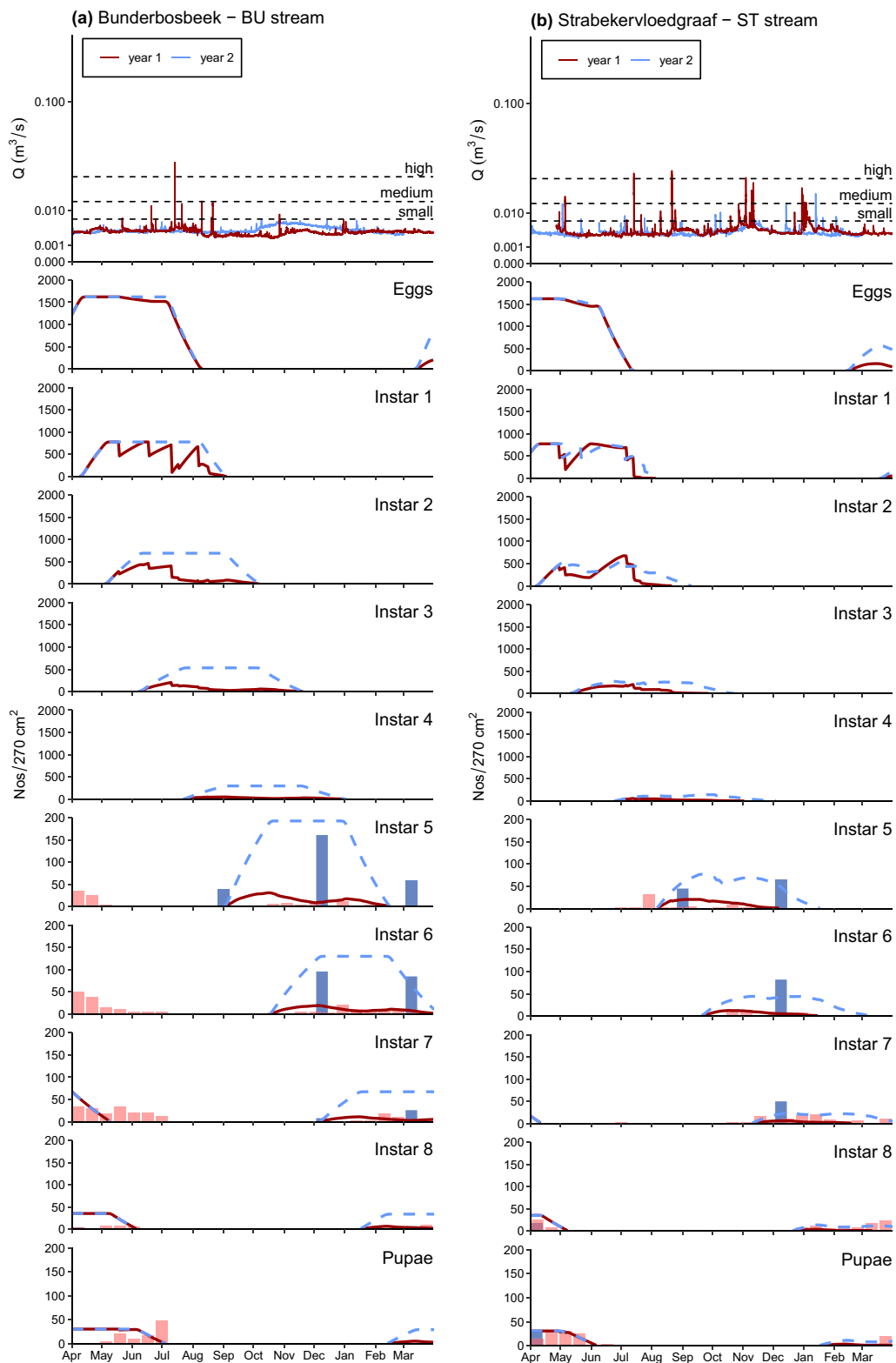


Fig. 4 Impact of discharge dynamics (Q) on *A. fuscipes* population densities during different life stages from April 2002–April 2004 in four streams **a** Bunderbosbeek (BU stream), **b** Strabekervloedgraaf (ST stream), **c** Seelbeek (SE stream), **d** Oude beek (OB stream). Measurements of population densities of larval instars 5–8 and pupae from year 1 are shown in red bars (sampled monthly) and from year

2 in blue bars (sampled every 3 months). The best fitting stage-structured population model, which assumes that the sensitivity of larvae to spates decreases with increasing larval stage, is shown for each aquatic life stage by a red solid line for year 1 and a blue dashed line for year 2. Note the discharge is in sqrt-scale and y-axis for stages egg-instar 4 is 10 times larger than instar 5-pupae

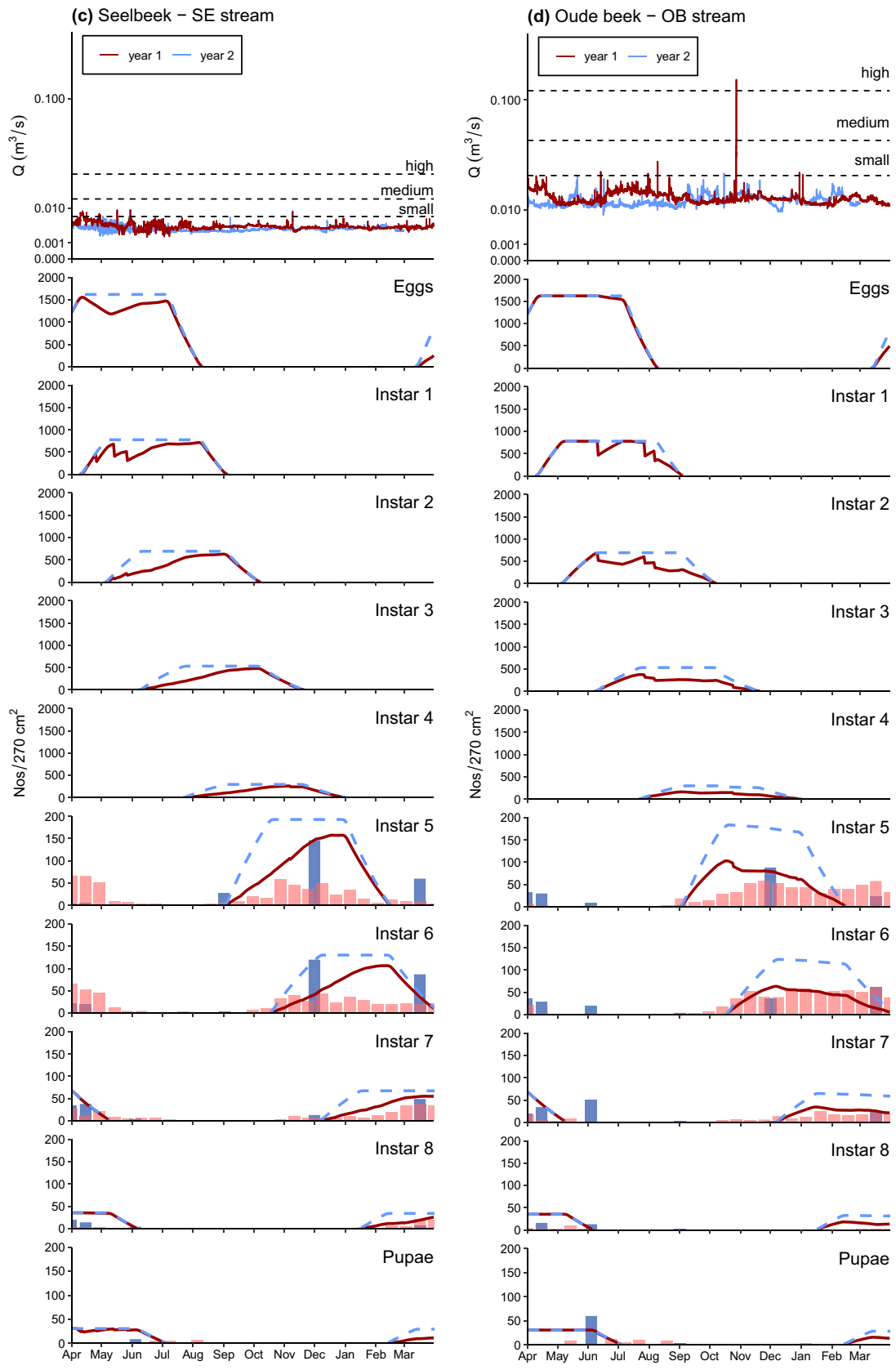


Fig. 4 (continued)

Table 1 Comparison of different model scenarios for the population density of larval instars 5–8 over two measurement years using the root mean square error (N = 32)

	Bunderbosbeek BU stream		Strabekervloedgraaf ST stream		Seelbeek SE stream		Oude beek OB stream	
	RMSE	Δ_i	RMSE	Δ_i	RMSE	Δ_i	RMSE	Δ_i
Constant low	160	133	162	137	130	80	117	68
Constant high	27	0	39	14	49	0	74	25
Decrease with stage	28	1	25	0	72	23	49	0
Increase with stage	134	107	66	41	64	15	92	43

Δ_i represents distance from the model with the lowest RMSE, and thus best fit

Similar to other aquatic ecological studies, the early life stages of *A. fuscipes* (larvae instar 1–4) were not sampled effectively in this study. The smallest larvae may have been present in a different (micro)habitat than the larger larvae, like the sand under the stones, as only the top layer of gravel was collected. Alternatively, they may have been mechanically damaged in the buckets during transport or passed through the sieve when sorting the samples, as the mesh of the sieve was larger than the head width of larval instars 1–4. To compensate for the ineffective sampling, we applied the stage-structured population model (i.e. StagePop), which proved to be a valuable tool to obtain an indication of the duration, timing and mortality patterns of the early life stages of *A. fuscipes* for which sampling was ineffective.

The natural life cycle of the population in the model was based on previously obtained parameter values, such as stage durations, of an un-impacted headwater stream in Central Germany. However, actual stage durations are dependent on water temperature and cohort (Castro 1975). This temperature dependency may have caused slight differences between the timing and duration of each life stage, potentially causing uncertainty in the sensitivity of the population model compared to the field situation. In future studies, the model could thus be improved by making each stage duration temperature dependent (Kettle and Nutter 2015). Additionally, in some streams (e.g. BU and SE stream) that were disturbed by peak discharges during the first year, the *A. fuscipes* population grew fast and recovered during the following stable year. Similar to previous studies, we observed a simultaneous presence of different life stages of *A. fuscipes* in each stream, which may spread the risk of high mortality to discharge peaks (Becker 2005). Nijboer (2004) proposed that after a reduction in the population density by hydrological disturbances, the remaining females may be able to lay more eggs than normal, as there is less competition for food. Such density-dependent processes would need to be studied further in experiments, and could be included in the model to gain a better understanding the influence of spates on the local extinction of populations. Despite these uncertainties in the stage-population model, we were able

to show that population declines may have been associated with the timing of spates, coinciding with the presence of early life stages.

Our study supports previous findings that floods can result in severe declines in stream invertebrate densities (see studies in Lake 2000; Death 2008). Although recovery from floods by invertebrates is typically high, some previous studies observed changes in species composition following repeated, severe and/or unpredictable flooding (e.g. Giller et al. 1991; Scrimgeour et al. 1988; Robinson et al. 2003). It is generally accepted that the effects of spates depend greatly on the taxon, as taxa have different resistance (ability to tolerate disturbance) and resilience to flow (ability to recover after a disturbance) (Death 2008; De Brouwer et al. 2017). This study provided initial indication that the resistance to peak discharge of invertebrates not only depends on the taxon, but also varies between life stages. This may have implications for management and restoration of freshwater ecosystems, as the current single-life-stage-based assessments with a strong focus on late instar or aquatic adult life stages may not elucidate which stressors or disturbances actually constrain invertebrate population densities during their entire life cycle, which may lead to unsuccessful management efforts. Restoration measures might aim at environmental factors relevant for late instars or aquatic adult life stages, which may not be the limiting life stage for that species (Bond and Lake 2003; Lancaster and Downes 2010). The assessment of the critical life stages of a specific species to specific disturbances may help to identify the actual cause for the presence and absence of species and thereby aid more effective management and restoration of degraded aquatic systems.

Acknowledgements We would like to thank Rebi Nijboer for coordinating the field work and preparing the data; Dorine Dekkers, Marie-Claire Boerwinkel, Ruud van Kats, Matthijs Bassie, Jennie van Iwaarden, Jasper Wijkamp and Dimitri Huntink for assistance with the fieldwork and measuring the head capsule widths of the caddisflies; Theo Jacobs, Rini Schuiling and Co Onderstal for digitalizing the substrate coverage; Isabel Smallegange for valuable discussions on population ecology models; Helen Kettle for writing an example model script in stagePop; Sven van der Lee for assisting with R; Staatsbosbeheer, Stichting Geldersch Landschap and several private landowners for

access to their properties. Two anonymous reviewers provided valuable suggestions to improve the manuscript.

Author contributions PV contributed to the study conception and design. Material preparation and data collection were performed by PV, RV and others (see Acknowledgements). GL performed the data analysis. The first draft of the manuscript was written by GL and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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