What to do if streams go dry? Behaviour of Balkan Goldenring (Cordulegaster heros, Odonata) larvae in a simulated drought experiment in SW Hungary

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Abstract. 1. In case of dryings, the hyporheic zone is one of the most important refugia for stream macroinvertebrate communities, including the few Odonata species living in these habitats, such as Cordulegaster species. There is no information on the desiccation resistance strategies and methods of any members of the genus, including Cordulegaster heros.

2. We hypothesised that the larvae use burrowing behaviour to survive droughts. In this study, beyond recording the survival rates of the larvae, we tested the effects of the sediment particle size and the body size of the larvae on burrowing behaviour in a 3-week-long simulated drought experiment in an indoor artificial stream system.

3. Eighty larvae were involved in the experiment, from which 60 were treated with drought, and 20 served as controls. Larvae were put into flowing water, into separate special compartments; 1 day later, the flow was ceased, and then, the water level was gradually decreased for 3 weeks.

4. Approximately 15% of larvae could survive the 3 weeks of drying. The survival probability of drought-treated larvae was significantly increased if animals burrowed into the sediment. In addition, the survival probability was higher in case of fine substrate material. Size of the larvae only affected the depth of the burrowing, not the survival rate.

5. However, two-thirds of the larvae did not dig into the sediment, which implies that surviving via burrowing is not the only mechanism of the species to withstand dry periods.

Key words. Anisoptera, artificial stream system, burrowing behaviour, climate change, stream-dwelling dragonfly, water deprivation.
bistonii-group’ sensu Boudot (2001) together with Cordulegaster heros Theischinger, 1979, it was suggested that especially larger larvae can survive dry periods in moist sediment under river channels (i.e. hyporheic zone) (Holusá et al., 2015).

The Balkan Goldenring (C. heros) is a charismatic species for conservation biology in Central and Southeastern Europe (Boda et al., 2015b). The species is endemic to the region, and its occurrence is restricted to a relatively small area (Boda et al., 2015a,b). It is listed in the Annexes II and IV of the EU Habitat Directive (EC, 1992) and in the Annexes I of the Bern Convention R6 (2011), and it is also a strictly protected species (Lang et al., 2001). Accordingly, Boda et al. (2015a,b) found C. heros specimens up to 4 cm deep in the sediment, while in case of other Cordulegaster species, larvae were found more than 10 cm deep (reviewed in Lang et al., 2001).

Taking into account that the preferred habitats of C. heros are very prone to drying (i.e. Mediterranean small headwater streams), the species is likely to possess some kind of drought resistance mechanism, and it is possible that larvae can utilise their burrowing behaviour to survive dry periods in the hyporheic zone (based on Holusá et al., 2015).

However, to our knowledge, no information exists on the exact desiccation resistance strategies and methods of any Cordulegaster species. Similarly, the number of experimental studies on the desiccation resistance of dragonfly larvae is very limited except for a few papers (Willey & Eiler, 1972; Rebora et al., 2007b), but all of these were focussed on pond-dwelling species.

Thus, based on the available information on the ecology of C. heros, we hypothesised that the larvae use burrowing behaviour to survive droughts. In this study, beyond recording the larval survival rates in a simulated drought, we tested the effects of the sediment particle size and the body size of the larvae on burrowing behaviour in a controlled laboratory experiment. Our specific questions were: How long can larvae survive after the cessation of flow? How deep can larvae burrow? How does substrate particle size affect the survival rates? Is there a difference between bigger and smaller larvae in behaviour?

Materials and methods

Laboratory population

Forty big (F and F-1 instar) and 40 small (F-2 and younger) C. heros larvae were collected for the experiment at the Ól-völgyi-stream located in the Mecsek mountains, SW Hungary (N46°15′ 49.00′′, E18°22′ 02.00′′) on 25 October 2018. Additional 5 and 5 specimens, respectively, were also transported to the lab for backup reasons. Big and small larvae were transported in separate buckets filled with water and some leaves from the stream. Several Gammarus fossarum Koch in Panzer, 1836 specimens were also added to the buckets to provide food for the larvae during transportation and acclimation. In the laboratory, larvae were given approximately 1 h of acclimation time until the temperature of the stream water and the tap water became equal. Before getting involved in the experiment, the wet mass of all larvae was measured with 0.01 g accuracy. All larvae were assigned to a ‘tube’ (details in Experimental design, Fig. 1b) randomly. Larvae in the experiment were not fed to exclude effects of hunting and feeding behaviour. It was proven earlier in a drying experiment that starvation did not significantly affect the survival rates of Odonata larvae (Rebora et al., 2007b). Backup and surviving larvae were stored in 20-litre plastic containers filled with aerated aged tap water and were fed ad libitum with frozen Chironomidae larvae. Sand, gravel, stones, and some leaves were provided for substrate. Big and small larvae were

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kept separate to avoid cannibalism. Surviving larvae were transported back to the original collecting location after the end of the experiment (20 November 2018) and were released after acclimation to stream water temperature. Deceased individuals were preserved in 96% ethanol and are stored in the Department of Hydrobiology, University of Pécs.

The collecting, transporting, maintaining, and releasing of the larvae of the strictly protected *C. heros* were carried out in accordance with the permission PE/KTFO/01675-9/2018, which was issued by the Department of Nature Conservation and Environmental Protection of the Government Office for Pest County.

**Experimental design**

The experiment was conducted in an indoor artificial stream system at the Department of Hydrobiology, University of Pécs. The system is 2.4 m wide and 8.0 m long, in which four small basins (0.8 m × 2.4 m) were created with separate buffer tanks (volume = 0.25 m$^3$) and pump systems (Fig. 1a). Three of these were treated with drought, while in the fourth one (control), continuous flow was maintained through the whole experiment. Flow was generated by three automated wastewater pumps per basin, which circulated the water from the end of the basin back to the buffer tank, from where the water was released into the beginning of the basin through three pipes (inner $\varnothing = 38$ mm).

Each basin contained 20 ‘tubes’ (Fig. 1b) (inner $\varnothing = 15.5$ cm, height = 28 cm, filled with 20 cm of substrate). Every ‘tube’ had six big holes ($\varnothing = 5$ cm, 20 cm from the bottom), which were covered with a hard plastic mesh (2 mm mesh size), and four small compensating holes ($\varnothing = 4$ mm, 5 cm from the bottom). The big holes allowed water to flow through the ‘tubes’, while the compensating holes let the inner water flow out from the ‘tubes’ when the outer water level was decreased. The bottom 5 cm of the substrate was wet through the whole experiment because of the location of the compensating holes (Figs 1b and 2h). The inside of each ‘tube’ was marked at every 2 cm with alcohol-based markers, forming a scale to make the measurements of the burrowing depths easier. Every ‘tube’ contained only one larva.

To test the effect of substrate particle size, we used fine sand (1–2 mm grain size) and coarse gravel (6–8 mm grain size) sediment types. Size categories were chosen in order to demonstrate the difference between a finer (which is close to the preferred mean substrate grain size of the species in natural conditions) and a coarser sediment. Natural, round-grained, pre-sorted quartz aquarium sand and gravel were used. All the substrate was washed thoroughly before use.

Based on the combination of the two larval sizes (S: small, B: big) and the two substrate particle sizes (F: fine, C: coarse), four treatment types (SF, SC, BF, BC) were created. We used complete block design, where one from each treatment created a block. Five blocks were put in one basin. Altogether, 15 blocks were treated with drought, and 5 blocks were kept as controls. Drought-treated larvae were sampled on three occasions in order to keep track of the mortality through the whole experiment. At every sampling time (details in Experimental schedule), five blocks (20 larvae) were randomly chosen. If the larva could not be seen on the surface, then the substrate was carefully removed in thin layers with a small aquaria net until the specimen was found. After that, the larva was put into water for a few minutes to rehydrate; then, the status of the animal (survived/dead) was recorded, and finally, its wet mass was measured.
measured. Surviving individuals were removed from the experiment because of the effects of disturbance and rehydration.

Soil moisture-measuring sensors (Meter Teros 12) were placed in four randomly chosen 'tubes', one from each treatment. Two sensors were installed in each selected 'tube', one at 6 cm (top) and one at 14 cm (bottom) deep in the substrate (Fig. 1b). Respectively, the sensors were named 'Coarse-top' (Ct) and 'Coarse-bottom' (Cb) in gravel and 'Fine-top' (Ft) and 'Fine-bottom' (Fb) in sand. Soil moisture data were recorded every hour via Meter Em50 loggers. Air temperature of the lab was maintained constantly at 18 °C, and the photoperiod was set to 12L:12D using an automated timer and daylight white (4000 K) LED tubes.

Experimental schedule

When we created the experimental schedule, we tried to implement the conceptual model introduced by Boulton (2003), which states that, when a drying occurs in a stream, there are some thresholds between critical stages (loss of lateral connectivity, loss of flow connectivity, loss of surface water, loss of hyporheic water), which makes the disturbance effect of a 'stepped' type. Therefore, the experiment was scheduled as follows: The artificial stream system was started without animals on day 1 (23 October 2018) (Fig. 2a). Each basin was filled with 25 cm of tap water, which was circulated for 2 days to age the tap water (Fig. 2a). Larvae were put into the ‘tubes’ on day 3 (Fig. 2b). One day later, the flow was ceased (Fig. 2c). Water level was decreased to the substrate level (20 cm) on day 6 (Fig. 2d). After the loss of surface water (ALW), water level outside of the tubes was reduced by 5 cm every 3 days, resulting in a decrease of the water level in the sediment in the tubes (Fig. 2e–g). The outer water level was completely removed on day 18 (Fig. 2h). The first sampling was performed on day 14, the second on day 21, and the last one on day 28, which was the end of the experiment. The control group was also sampled on the last day, and it was treated as a separate sampling occasion in statistical tests. The drought period lasted for 3 weeks ALW.

Data analysis

To reveal if there is an association between the numbers of surviving and deceased larvae and sampling occasions (first, second, third, and control groups included), contingency tables were created, and $\chi^2$ tests for independence were used. To compare the wet masses of the larvae before and at the end of the experiment, paired Wilcoxon sign-rank tests were conducted. The survival probability of larvae in different treatments were compared by Kaplan–Meier survival analyses, combined with log rank $\chi^2$ tests, to find significant differences between the curves. The Mann–Whitney $U$-test was used to compare the burrowing depths of control and drought-treated larvae, big and small larvae, and larvae on coarse and fine sediment. To find differences among the burrowing depth of the four treatment types, the Kruskal-Wallis test was used, combined with the Mann–Whitney pairwise post-hoc tests.

To give an overview on the influence of drought treatment, burrowing depth, sediment type, and larva size on the survival and to better visualize our results, decision trees were created. The decision tree method results in a tree-like classification model, which groups cases (larvae) into classes of the dependent variables based on values of the independent variables. Two decision trees were created, both with the Chi-squared automatic interaction detection (CHAID) growing method, likelihood ratio $\chi^2$ statistics for small sample sizes, Bonferroni-adjusted significance values, and 20 cases as minimum values for nodes. The dependent variable was survival (nominal, categories: survived and died) for both models. The first model specification included drought treatment (nominal, categories: drought and control), burrowing depth (scale), sediment type (nominal, categories: fine and coarse), and larva size (nominal, categories: big and small) as independent variables, while the second model included only drought treatment, sediment type, and larva size. Drought treatment was forced as the first splitting variable to separate drought-treated and control larvae first.

All statistical analyses, except decision trees, were conducted in PAST ver. 4.0 (Hammer et al., 2001). Decision trees were created in IBM SPSS Build 1.0.0.1327. (IBM Corp, 2019).

Results

Soil moisture

At the beginning of the experiment, all soil moisture sensors measured 0.40–0.44 m$^3$ m$^{-3}$ wetness when the sensors were under the water level. When the water level decreased to 10 cm (day 12), which was 4 cm below the top sensors, the measured values were <0.1 m$^3$ m$^{-3}$ in the case of Ct and 0.29–0.33 m$^3$ m$^{-3}$ in the case of Ft sensors. The soil moisture measured by Ft sensors decreased to <0.1 for m$^3$ m$^{-3}$ 3 days later (day 15), when the water level decreased to 5 cm. On the same day, bottom sensors were also exposed above the water level by 1 cm. Measured values by Cb sensors decreased to <0.3 m$^3$ m$^{-3}$, while the wetness of fine sediment remained above 0.4 m$^3$ m$^{-3}$ at this depth. The soil moisture value for Fb sensors started to decrease when the outer water level reached 0 cm (day 18), and it gradually dried to <0.1 m$^3$ m$^{-3}$ in 7 days (Fig. 3).

Survival probability

From the 60 larvae that were treated with drought, 29 survived. At the first sampling (8 days ALW), the mortality was 20%; on the second (15 days ALW), it increased to 50%; and at the final sampling (22 days ALW), 85% of the sampled 20 larvae were dead. From the 20 control larvae, only 2 died, both at the beginning of the experiment (on days 4 and 7). $\chi^2$ test for independence showed significant association between the numbers of dead and surviving larvae and sampling occasions (control group included, $\chi^2 = 28.214$, Fisher’s exact $P < 0.001$).

The wet mass of the larvae significantly decreased in the case of the second ($W = 151$, exact $P < 0.001$) and third ($W = 209$, exact $P < 0.001$) samplings and in controls ($W = 63.5$, exact $P = 0.005$), but there was no significant change in the mass of
the specimens at the first sampling ($W = 103$, exact $P = 0.072$). There were also significant differences between the starting and the sampling masses of surviving ($W = 554.5$, $P < 0.001$) and deceased ($W = 434$, $P < 0.001$) animals.

The survival rate of control and drought-treated larvae were compared by Kaplan–Meier survival analysis, where the log rank $\chi^2$ test showed that the drought significantly lowered the survival probability of the larvae ($\chi^2 = 8.4824$, $P = 0.004$) (Fig. 4a). When we compared the four treatment types (Fig. 4b), the survival probability of the BF larvae was significantly higher than both BC ($\chi^2 = 7.262$, $P = 0.007$) and SC ($\chi^2 = 6.3046$, $P = 0.012$). If larvae size and sediment particle size are treated separately, then the results are as follows: There were no differences between small and big larvae ($\chi^2 = 0.47607$, $P = 0.490$) (Fig. 4c), but the survival probability of the larvae on coarse sediment was significantly lower compared to the ones on the fine sediment ($\chi^2 = 7.8349$, $P = 0.005$) (Fig. 4d). The larvae that burrowed into the sediment significantly increased their survival probability ($\chi^2 = 26.808$, $P < 0.001$) compared to the ones that did not dig (Fig. 4e).

In addition, we did not observe any emergence through the whole experiment, but there were several larvae that tried to escape the ‘tubes’ by walking in circles along its wall and sometimes by climbing up on the mesh.

Burrowing depths

We could measure burrowing depths in case of 21 drought-treated (mean = 1.4 cm, max = 3 cm, SD = 0.8 cm) and 9 control (mean = 0.8 cm, max = 2 cm, SD = 0.7 cm) larvae.

The drought-treated larvae dug significantly deeper ($U = 50.5$, $P = 0.040$) (Fig. 5). However, most of the larvae (65%) that were involved in the drying did not burrow. There was only one larva that burrowed into the substrate and did not survive the experiment (death registered on day 28, the last day of the experiment). All other (20) drought-treated larvae that chose to dig survived. There was a significant difference among the four treatment types in burrowing depths ($H = 12.95$, $P = 0.003$). BF larvae dug significantly deeper than all other treatment combinations (BF-BC: $U = 10$, $P = 0.041$; BF-SF: $U = 12$, $P = 0.008$; BF-SC: $U = 0$, $P = 0.010$) (Fig. 5). None of the small larvae burrowed on coarse sediment (Fig. 5). If larvae size and sediment particle size are treated separately, then the results are as follows: Bigger larvae dug significantly deeper than small larvae ($U = 28$, $P = 0.002$), and larvae on fine sediment could burrow deeper than the ones on coarse substrate. Although the later finding seemed to be clearly visible, statistically, it is only marginally significant ($U = 40$, $P = 0.051$).
Fig 5. Violin and box plots of the burrowing depths of the surviving control (blue) and surviving drought-treated (orange) larvae in the four treatment types shows that larvae dug deeper in case of water deprivation, and also, bigger larvae size and finer substrate are in favour of deeper burrowing. No small larvae burrowed on coarse sediment. BC, big larvae on coarse sediment; BF, big larvae on fine sediment; SF, small larvae on fine sediment; SC, small larvae on coarse sediment; ○, interquartile range; –, median; T, minimum and maximum values; violin, kernel density plot. [Colour figure can be viewed at wileyonlinelibrary.com].

Importance of independent variables on the survival

For the first decision tree model (Fig. 6a, specifications: survival as dependent variable, drought treatment, burrowing depth, sediment type, and larvae size as independent variables), the CHAID method included drought treatment and burrowing depth in the resulting model as independent variables. Drought treatment was the first splitting variable that significantly influenced \( \chi^2 = 12.327, P < 0.001 \) the survival. Of the drought-treated larvae, 51.7% did not survive, while this was only 10% in case of control larvae. The survival of drought-treated larvae was influenced significantly \( \chi^2 = 32.934, P < 0.001 \) by burrowing depth. Of larvae that did not burrow, 76.9% died, while only 4.8% of burrowing larvae did not survive the experiment.

A second model (Fig. 6b) was created without burrowing depth to visualize the significance of the other independent variables on drought-treated larvae. This time, the drought treatment and sediment type were chosen as the independent variables, which had a significant effect on survival. The first splitting was the same as for the first model. Sediment type was the second splitting variable, which had significant influence \( \chi^2 = 5.491, P = 0.019 \) on the drought-treated larvae. Two-thirds of larvae (66.7%) died on coarse sediment, but only 36.7% of larvae died on fine sediment.

The overall percentage of correctly classified cases were 85% for the first model and 71.3% for the second model.

Discussion

In this study, we examined the survival probability and burrowing behaviour of *C. heros* larvae in a 3-week-long simulated drought experiment in an indoor artificial stream system. Our main aim was to find out how *C. heros* larvae can withstand dry periods in streams *in situ* and how that is affected by the sediment particle size and the size of the larvae. We found that larvae can survive 3 weeks without surface water, especially if they chose to burrow into the moist sediment instead of using another strategy (i.e. trying to escape or staying on the surface). The survival probability is higher in case of finer substrate, most probably because it stays wet for longer, and larvae, especially bigger ones, can burrow into it more easily, which also increases their survival probability.

With the progress of drying, as was expected, the soil moisture decreased more suddenly and much faster in coarse gravel sediment than in fine sand substrate. The sensors in fine sediment could measure high soil wetness values even in cases when the outer water level was below the devices. This is most probably due to capillary action, which is more prominent in sandy substrate where the pore size is much smaller between particles than in case of coarse gravel substrate.

As the severity of the drought was increasing (i.e. the water level was decreasing in the sediment), the mortality of the larvae also rose. However, 15% of larvae could survive the whole 22 days ALW.

The mass of larvae did not decrease notably at the first sampling (day 14); however, the mortality rate was already higher (20%) at this time than in the control group (10%) at the end of the experiment, where the wet mass of larvae decreased significantly. These results suggest that the mortality of the drought-treated larvae was not attributed to starvation. Accordingly, Rebora *et al.* (2007b) found no difference between the Kaplan–Meyer survival curves of fed and starved controls when they studied the water deprivation tolerance of *Libellula depressa* Linnaeus, 1758.

The survival probability of *C. heros* larvae was significantly increased in case of fine substrate material. However, the size of larvae did make a difference only between BF and SF larvae when we compared all four treatment types at the same time. Survival probability was also strongly dependent on burrowing behaviour. These findings are strengthened by the results of the decision tree models: survival of the drought-treated larvae was significantly influenced by burrowing depth and also by the sediment type.

As for burrowing depth, size of the larvae made a significant difference: bigger larvae could dig deeper than small ones. In addition, finer sediment allowed larvae to dig deeper, which is in accordance with the findings that *C. boltonii* (Donovan, 1807) larvae in natural conditions burrowed into fine sediment (grain particle size <0.25 mm), while on coarse sediment (grain particle size ~8 mm), they were almost completely uncovered (reviewed in Lang *et al.*, 2001). Our result, that no small larvae were observed burrowing into coarse sediment, could be connected with the findings of Boda *et al.* (2015b), that small larvae prefer patches with higher proportion of fine sediment types.

Larvae that chose to burrow significantly increased their chance to withstand the drought alive. Interestingly, a bigger proportion of control larvae (45%) burrowed than drought-treated larvae (35%), but the burrowing depths were significantly deeper in the case of drought-treated specimens. Our results concur with the findings of Lang *et al.* (2001),...
who observed that 41–90% of *C. heros* larvae are burrowed in the sediment in natural conditions. In addition, several studies (Buchwald, 1988; Böcker, 1993; Heidemann & Seidenbursch, 1993; Boda et al., 2015b) agree that the collection of *C. heros* larvae is especially hard in cold winter months because the larvae dig into the sediment much deeper. The maximum burrowing depth we measured was 3 cm, which is close to the maximum 4 cm that larvae dig in winter in natural conditions (Lang et al., 2001). It is possible that this deeper burrowing behaviour is a result of suboptimal abiotic conditions, and it can be triggered not only by cold temperature but also by water deprivation.

On the other hand, 65% of larvae did not burrow into the sediment; instead, several larvae were observed in the act of trying to escape the experimental ‘tubes’. Piersanti et al. (2007) found very similar behaviour in case of *L. depressa* larvae: When the experimental pools were close to loss of surface water, the larvae of *L. depressa* began to leave the ponds and tried to find other refugia. It was also shown for *L. depressa*, that larvae can walk on dry ground for more than 60 m (Piersanti et al., 2007), and they are able to find water by sensing air humidity with hygroreceptors (Rebora et al., 2007a,b). In addition, Rebora et al. (2007b) found that, at 100% relative air humidity, larvae of *L. depressa* tend to emerge. This kind of connection between very high air humidity and emergence is not yet confirmed for *C. heros*, but we did not record any emergence in our experiment despite several last stadia (F) instars being involved, and the air humidity must have also been high in the lab because there was some excess water in the basins, buffer tanks, and in the control channel. Unfortunately, air

**Fig 6.** The results of the two decision trees show that drought significantly influences the survival of *Cordulegaster heros* larvae, and the survival of drought-treated larvae is influenced by burrowing depth (a) and also by sediment type (b). Models were created with CHAID growing method, likelihood ratio χ² statistics, and Bonferroni-adjusted significance values. The percentage together with the sample sizes (n) of survived (blue) and dead (orange) larvae are shown in each node. (a) First model (independent variables: drought treatment, burrowing depth, sediment type, larvae size). (b) Second model (independent variables: drought treatment, sediment type, larvae size). Correctly classified cases are 85% for (a) and 71.3% for (b). [Colour figure can be viewed at wileyonlinelibrary.com].

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humidity and the exact methods of escaping behaviour was not measured/recorded in our experiment because the focus of our study was on the burrowing behaviour of the species. However, it is possible that *C. heros* larvae are also in possession of some kind of receptors, which makes them able to sense humidity, and as they were aware of water outside the ‘tubes’, they tried to reach it. But this kind of refugia searching mechanism should be tested in controlled experimental conditions in the future.

Considering that the population from where the individuals were collected is in a hilly region with temperate climate, it is also possible that most of these larvae are not fully adapted to tolerate dryings. The range of the species spans from the Mediterranean to the colder mountainous regions of the Western Carpathians. This may imply that populations occupying different geographical regions may have different coping mechanisms to withstand droughts. It is possible that the deeper burrowing behaviour of the species is triggered by different environmental factors (i.e. cold temperature or water deprivation) in different ecoregions. However, more singular studies or an international collaboration is needed with partners from different parts of the range of the species across ecoregions in order to obtain a deeper understanding on the triggering mechanisms of aestivation by burrowing. Laboratory experiments are suggested to be carried out with similar methods to our study with populations that inhabit different types of waters (e.g. intermittent and perennial streams) from different climatic zones. Moreover, the humidity-sensing and refugia-searching mechanisms of the species should be tested with similar methods to Rebora *et al.* (2007b).

Moreover, with the ongoing climate change, it is expected that the area where the laboratory population was originated from will shift towards a drier and warmer climate (based on Beck *et al.*, 2018). This will change the formerly perennial watercourses to an intermittent flow regime (Datry *et al.*, 2017), and the frequency and magnitude of drying events will increase (Hoegh-Guldberg *et al.*, 2018), which will create more challenges for the population in the future. Taking into account that more than 80% of larvae could die in a 3-week-long drought (which can be considered a short period of time compared to the length of the larval development), multiple and/or prolonged drying events could lead to range shift or even local extinction of populations. On the other hand, the changing climate can also lead to adaptation of the species to warmer temperature and droughts. This could mean, for example, shorter life cycle, faster larval growth, and changes in voltinism and in body size (reviewed in Wonglersak *et al.*, 2020). It is also possible that the Mediterranean population (which are probably better adapted to droughts) could expand to the Northern areas.

Overall, a proportion of the larvae of the species are capable of surviving even 3 weeks without surface water under laboratory conditions, but the probability of survival is strongly affected by burrowing behaviour and the quality of the substrate, while the size of the larvae only affects the burrowing depths. Of larvae that burrowed into the sediment, 95% could survive the experiment. On the other hand, more than half of the larvae (65%) did not dig into the sediment, which implies that surviving via burrowing is not the only mechanism of the species for withstanding dry periods.

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**Data availability statement**

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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