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Impacts of Habitat Management on Larvae of the Damselfly *Coenagrion mercuriale* (Coenagrionidae, Odonata)—A Laboratory Study

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ABSTRACT

Habitat management of small lotic waterbodies is essential to maintain flow and the quality of the habitats. For this purpose, aquatic plants are typically removed by authorities. This is done in a more or less disruptive manner, depending on the risk of interference with the bed. Since small lotic waterbodies are biodiversity-rich habitats, the effects of habitat management on macroinvertebrates need to be analyzed. In particular, we analyzed aquatic plant preferences, tolerance to sediment burial, and thanatosis to derive recommendations for current habitat management. A habitat choice experiment with larvae of the threatened damselfly *Coenagrion mercuriale* was conducted to identify preferences between four different aquatic plants, namely *Callitriche* spp., *Elodea canadensis*, *Phragmites australis*, and *Veronica beccabunga*, which are all typical *C. mercuriale* larval habitats. We aimed to investigate if specific aquatic plants should be avoided when removing aquatic vegetation during habitat management. In addition, we analyzed two further habitat management scenarios on larvae of *C. mercuriale*: fine sediment burial and thanatosis (reflex immobilization), which can both be induced by management machines. The habitat choice experiment showed no significant preferences for specific aquatic plants except for the direct comparison of *V. beccabunga* and *Callitriche* spp. We found that the majority of the larvae were tolerant to sediment burial of 1 cm; tolerance to thicker layers was rare. On absorbent paper, thanatosis duration differed between in-water and out-of-water. Larvae out-of-water stayed in thanatosis for longer, increasing the risk of predation when being removed with aquatic plants during management. The present study shows that different habitat management activities have impacts on *C. mercuriale* larvae. These impacts should be considered when choosing and performing appropriate management activities in small lotic waterbodies.

1 | Introduction

Habitat management affects freshwater organisms by direct impacts as a result of the removal of aquatic macrophytes, i.e., habitats of several taxa (Kaenel et al. 1998), or by the removal of biomass on cut weed (Dawson et al. 1991). There are further relevant side effects, such as changes in hydrology (Kaenel et al. 1998), mobilization of suspended sediments (Old et al. 2014), or drift (Kern-Hansen 1978).

Many macroinvertebrates need distinct vegetation, such as the phytobiotic larvae of the damselfly *Coenagrion mercuriale* (Charpentier 1840). They are strongly associated with submerged vegetation (Thelen 1992; Buchwald 1994) during their one to two years life cycle as aquatic larvae in their development period between August and May (Wildermuth and Martens 2019). Previous studies identified species of the plant association Raununculo trichophylli-Sietum submersi Th. Müller 1962 as necessary for the occurrence of *C. mercuriale*

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(Buchwald 1994). In particular, plant species with both submerged and emerged parts are preferred as a microhabitat by *C. mercuriale* larvae, especially *Nasturtium officinale* and *Phalaris arundinacea* (Thelen 1992). Macroinvertebrate species in specific plants as microhabitat have been studied previously by analyzing the relationship between macroinvertebrates and aquatic plant (leaf) structures (e.g., Balci and Kennedy 2003; Harrod 1964; Krecker 1939; Shiel 1976; Quade 1969).

The removal of aquatic macrophytes destroys important microhabitats in small lotic waterbodies, such as those of *C. mercuriale* larvae, although habitat quality is increased by preventing silting up and overgrowth. In addition, the removal of aquatic macrophytes can be the explicit aim of habitat management. This can, for example, be the reason for the management or the removal of non-indigenous aquatic macrophytes, such as *Elodea* spp., to ensure native plant biodiversity. Non-indigenous aquatic macrophytes increase habitat complexity and stabilize substrate, although their growth rate can negatively affect macroinvertebrate and fish communities (Schultz and Dibble 2012) as well as native plant species richness (Stiers et al. 2011). Nevertheless, the negative impact of non-indigenous aquatic macrophytes on macroinvertebrates in lotic systems and small waterbodies has not been well studied (Tasker et al. 2022) and should be investigated with regard to *C. mercuriale* larvae.

In addition to macrophyte habitats, the bed of small lotic waterbodies provides habitats for a wide range of taxa including Ephemeroptera, Plecoptera and Trichoptera (EPT), Odonata (e.g., Gomphidae), lamprey, fish (e.g., *Misgurnus fossilis*), and mussels (e.g., *Unio crassus*). Both microhabitats (macrophytes and bed) are affected by sediment deposition, which affects *C. mercuriale* larvae. The natural deposition of sediment in lotic systems is primarily caused by bed/bank erosion and overland flow (Droppo et al. 2015). Moreover, anthropogenic drivers such as climate change or food production cause increasing sediment transport (Song et al. 2020), as well as the management of waterbodies. The removal of macrophytes leads to erosion and downstream transport of fine sediments due to fluvial dynamics after their removal (Greer et al. 2017). Furthermore, Old et al. (2014) discovered that weed cutting mobilizes suspended sediment in the short term, which may have negative impacts on invertebrates by burying benthic surfaces.

Previous studies identified sedimentation as a possible negative factor, impacting invertebrate density and richness (Quinn et al. 1992; Rabení et al. 2005). The deposition of sediment causes multiple stressors on species, including chemical stress via lack of oxygen, indirect stress via habitat availability, food availability and quality, food web changes, and physical effects via abrasion, clogging, substrate composition, and burial (Jones et al. 2012). Burial increases mortality due to reduced access to food but mainly because of a reduced supply of oxygen (Jones et al. 2012). Response behavior to burial has been studied for assorted taxa, including EPT, Amphipoda (Conroy et al. 2018; Wood et al. 2005), and Gomphidae (Odonata) (Tobias 1995; Suhling and Müller 1996).

Despite direct impacts of habitat management, such as sedimentation and removal of aquatic plants, indirect impacts can also be provoked, such as increased drift rates or thanatosis. Kern-Hansen (1978) analyzed the effect of weed-cutting on the amphipod species *Gammarus pulex*, which showed increased drift. Drift is also induced by the mobilization of moving particles (Culp et al. 1986) and avoidance reaction to sediment (Rosenberg and Wiens 1978) i.e., consequently the escape to burial effects. Thanatosis might be provoked during habitat management since it is triggered by, among others, mechanical stimuli (Wildermuth 2000). Thanatosis describes reflex immobilization due to perennial contraction, also known as 'feigning death' (Wildermuth 2000). It increases survival after being attacked (Gyssels and Stoks 2005) and is known from several animal taxa (Humphreys and Ruxton 2018), including dragonfly (Williams and Dunkle 1976; Henrikson 1988; Wildermuth 2000) and damselfly larvae (Gyssels and Stoks 2005). However, movement by the current while in thanatosis could decrease survival rate due to predation (Otto and Sjöström 1983). To this date, it is yet unknown if thanatosis is induced by the equipment used in habitat management or due to an avoidance reaction following sediment deposition.

The present study aimed to analyze several impacts of habitat management on *C. mercuriale* larvae. The damselfly is a characteristic species for small lotic waterbodies and is dependent on habitat management that maintains habitat quality without destroying a great number of microhabitats. With the habitat choice experiment, preferences for four different aquatic plants were analyzed. In this study, the habitat choice experiment should reveal if *C. mercuriale* larvae have a preference for specific aquatic plants; if so, these aquatic plants should be avoided during habitat management—for example, by not removing them (since it is more likely that the larvae are sitting on them, which the experiment should show).

In addition, two different impacts of habitat management on larvae of the threatened damselfly *C. mercuriale* were analyzed: fine sediment burial and thanatosis. As previously described, sediment burial is known to reduce the survival of several macroinvertebrate taxa. The survival of Zygoptera larvae with regard to sediment burial has not been identified up to this point and was analyzed at three different sediment burial depths. Thanatosis is known for several animal taxa and was analyzed for *C. mercuriale* larvae as additional stress due to habitat management. The results were then discussed in the context of habitat management, considering possible impacts.

2 | Methods

2.1 | Sample Collection

Between August 2021 and October 2022, 97 *Coenagrion mercuriale* larvae (stadia F0 to F-5) were collected from two small lotic waterbodies in the southeast of Rhineland Palatinate, Germany: the Schmiedbrunnengraben (49°01′13.7″ N 8°11′09.8″ E) in Büchelberg, Wörth am Rhein; and the Vorderbach (49°03′18.8″ N 8°04′18.7″ E) in Schaidt, Wörth am Rhein. The larvae were kept individually in small containers (7 × 6 cm) with gravel and tap water (depth 1.5 cm, water volume ca 50.4 mL). To maintain the water quality and oxygen level for the lotic larvae, the water was changed every 2–3 days. The larvae were fed with *Daphnia* spp. and *Chironomus* spp. larvae. Prior to each experiment, all larvae were given the same feeding opportunity. The larval stage was classified according to Corbet (1955). Critical experiments like the sediment burial experiment (Experiment 2) were undertaken, ensuring that no larva died during the experiment; this is because *C. mercuriale* is a damselfly of high conservation status. After the experiments, larvae were placed back in their origin waterbody after recovery.

2.2 | Experiment 1: Habitat Choice

Habitat choice was analyzed with a pairwise experimental setup in rectangular containers (Figure 1). Four different aquatic plant habitats were used: *Callitriche* spp. (C), *Elodea canadensis* (E), *Phragmites australis* (P), and *Veronica beccabunga* (V), resulting in six different containers (CxV, CxE, CxP, ExP, ExV, PxV). The plant species were selected based on the plant association Raununculo trichophylli-Sietum submersi Th. Müller 1962, which has been identified as a habitat requirement for *C. mercuriale* larvae (Buchwald 1994). These include the species *V. beccabunga* and *Callitriche* spp., which are native to Germany. *E. canadensis* of the same plant association was also included as it is a non-indigenous species that is highly relevant in habitat management plans (Idilbi et al. 2024). We added *P. australis* to the group of tested plants as it is similar in plant structure to *Phalaris arundinacea*. *P. arundinacea* was previously identified as an important microhabitat for *C. mercuriale* larvae (Thelen 1992).

Every aquatic plant habitat occupied an area of 9 x 9 cm. Water depth in the container was 16 cm from the bottom and 7 cm from the plant pot surface as an artificial bed. The temperature was held constantly at 20°C–22°C, day and night.

Forty-five *C. mercuriale* larvae of stadia F0 or F-1 were placed individually on sand in the lid (Ø 4.6 cm) of a small cup with some water to acclimate. After 5 min, one lid (=one larva) was placed in each of the experimental containers to avoid intraspecific disturbance and possible cannibalism.

Each larva was kept for 24 h in the experimental container. Afterwards, the location of the larva was noted, and the larva was placed back into its small container or into the experimental container with the other two aquatic plants. Larvae were only placed in another experimental container with the same aquatic plant after at least 24 h to avoid preference for the previously selected habitat.

2.3 | Experiment 2: Fine Sediment Burial

C. mercuriale larvae were placed individually on 1 cm of fine sediment (sand, grain size 0.063–2 mm in line with DIN 4188/ISO 3310-1) in a small cup (Ø 4.1 cm) with some water to acclimate. After 5 min, fine sediment was added with varying layers (1 cm, 2 cm, 3 cm), tested for each larva with at least 3 h between each height. Following Conroy et al. (2018) and Wood et al. (2001), two

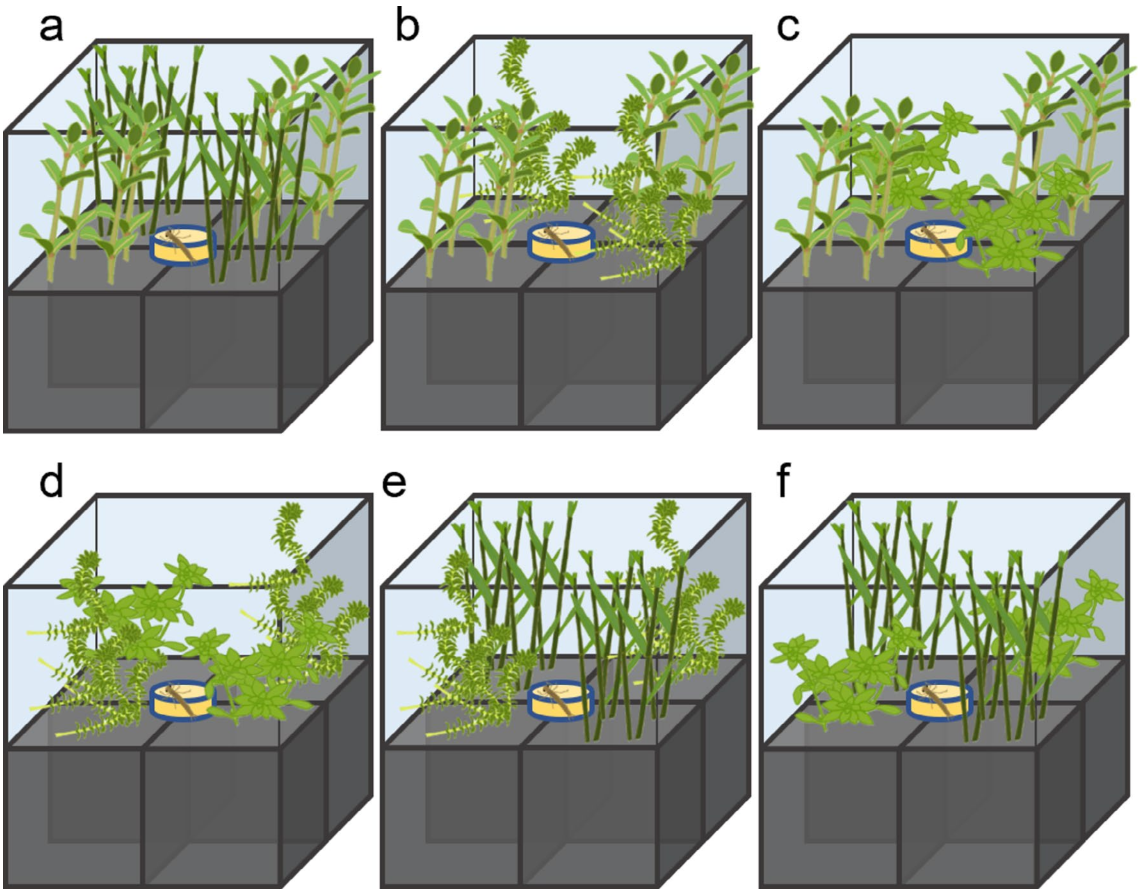

FIGURE 1 | Set-up of the pairwise habitat choice experiment with larvae of *C.mercuriale* (1a: PxV, 1b: ExV, 1c: CxV, 1d: CxE, 1e: ExP, 1f: PxC). [Color figure can be viewed at wileyonlinelibrary.com]

response times were recorded: 1. time the individual becomes visible above the sediment surface, in our study 'first appearance'; 2. time of complete excavation of the body, 'body appearance'. In contrast to Conroy et al. (2018) and Wood et al. (2001), the term 'appearance' instead of 'emergence' is used, since emergence for Odonata is known as term for larva/imago metamorphosis.

To avoid death due to lack of oxygen supply, the experiment duration was set to 30 min. If larvae did not excavate themselves within the given time, the measured time was set to 30 min. After the experiment, the larvae were placed back into their small containers with fresh water.

The experiment was conducted with F0 to F-1 larvae (first stadia class), F-2 to F-3 larvae (second stadia class), and F-4 to F-5 larvae (third stadia class). Burial behavior was recorded with a digital camera (DSC-WX350, Sony).

2.4 | Experiment 3: Thanatosis

Thanatosis duration and predation reactions were measured based on experiments by Wildermuth (2000) and Henrikson (1988). The larvae were grabbed at the thorax laterally with a tweezer and turned onto their back, (i) in water and (ii) out of water on absorbent paper. Additionally, (iii) a fish attack was simulated by pumping three times on the back of the larvae with a pipette with a wide opening (Ø 4 mm) (Henrikson 1988). Posture and time during thanatosis were noted. Thanatosis was defined as terminated when the first clear leg movements occurred.

Between the three partial experiments, there was at least a 15 min break for each larva. The same larvae were used for all experiments, all 38 larvae of stadia F0 or F-1. The thanatosis experiment was performed in daylight with water at room temperature and was recorded with the digital camera DSC-WX350 (Sony).

2.5 | Statistical Analysis

To test the preferences for a specific aquatic plant during the pairwise experimental set up in Experiment 1 "habitat choice", a binomial test was applied as the pairwise experimental set up provides dichotomous data (at the plant or not at the plant) and to analyze the theoretically expected distribution of observations. Differences between appearance signs (1. first appearance, 2. body appearance) and two groups of stadia class in Experiment 2 "fine sediment burial" were tested using a Chi squared test since the larvae were used only once (unpaired sample) and the experiment was terminated after 30 min so values "excavating/not excavating" were given. Effect size was tested with Cramer's V. To test the difference between times of the two partial experiments (i) thanatosis in-water and (ii) thanatosis out-of-water on an absorbent paper of Experiment 3, a non-parametric Wilcoxon signed rank test was applied. This test was used as the same larvae were used for both partial experiments (paired sample) and normal distribution requirement was not met, which was tested with the Kolmogorov–Smirnov test. Effect size was tested with Cliff's Delta.

Statistical analysis and graphical presentation were performed with Excel and R (R Core Team 2022). In R, the packages ggplot2 (Wickham 2016), gridExtra (Auguie 2017), readxl (Wickham and Bryan 2022), egg (Auguie 2019), ggpubr (Kassambara 2020), scales (Wickham and Seidel 2022), reshape2 (Wickham 2007), dplyr (Wickham et al. 2022), and ggpattern (FC et al. 2022) were used for the preparation of the figures. To test significance, binomial tests (habitat choice), t-tests (sediment), and a Wilcoxon test (thanatosis) were performed with base R (R Core Team 2022) and the package readxl (Wickham and Bryan 2022).

3 | Results

3.1 | Habitat Choice

The first experiment indicated that *Coenagrion mercuriale* larvae selected *Veronica beccabunga* significantly more frequently than *Callitriche* spp. (Binomial test ($n = 25$), $n(V) = 20$, $n(C) = 5$; $p = 0.004$) (Figure 2). The larvae in the other pairwise experimental containers did not show any significant habitat choice preferences. In addition, some larvae did not select any aquatic plant during the experiments, but did remain at or under the pot, at or on the lid, or on the bottom of the container. Regarding habitat

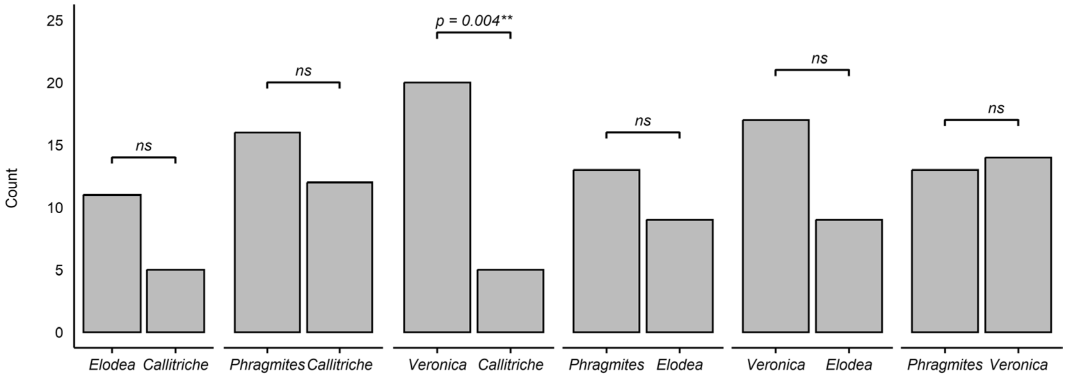

FIGURE 2 | Habitat choice of *Coenagrion mercuriale* larvae within 24 h in pairwise aquatic plants experiments. Preferences for a special aquatic plant were only significant for *Veronica beccabunga* in direct comparison with *Callitriche* spp., which has a stable stem compared to the flexible plant *Callitriche* spp. ns = non-significant.

microstructures, a higher count was observed for those habitats with stems of stable character. For the experimental container with *Elodea canadensis* and *Callitriche* spp., only 16 larvae out of 45 selected a plant ($n(C)=5$, $n(E)=11$), whereas the other larvae preferred the pot or the ground of the container. For the other experimental containers including at least one plant with a stable stem character (*P. australis* and *V. beccabunga*), between 22 and 28 larvae out of 45 larvae selected a plant rather than the pot or the ground (P/C $n=28$: $n(P)=16$, $n(C)=12$; C/V $n=25$: see above; P/E $n=22$: $n(P)=13$, $n(E)=9$; V/E $n=26$: $n(V)=17$, $n(E)=9$; P/V $n=27$: $n(P)=13$, $n(V)=14$).

3.2 | Sediment Burial

Due to the low excavation success for 2 and 3 cm of burial (Figures 3 and 4), and because the experiment was stopped after 30 min, significance testing was run only for 1 cm between stadia F0/F-1 and F-2/F-3 and only if the larvae excavated themselves (yes/no) during the given time. There was a significant difference between showing first signs with head/caudal lamellae between the stadia F0/F-1 and F-2/F-3 ($X^2(1)=4.1761$, $p=0.041$, $V=0.3015$). However, there was no significant difference for the excavating success between the two stadia during the given time ($X^2(1)=1.9841$, $p=0.159$, $V=0.2182$).

For the head/caudal lamellae appearance and body appearance, a tendency of increasing time between the three burial depths was observed (Figures 3 and 4), yet it was not statistically tested as the experiment was terminated after 30 min. For stadia F0/F-1, the length of time for body appearance varied more than for head/caudal lamellae appearance. In addition, a tendency of increasing time for smaller larvae stadia was observed for a burial depth of 1 cm. For a burial depth of 2 cm, more larvae of stadia F-2/F-3 excavated themselves than those of stadia F0/F-1.

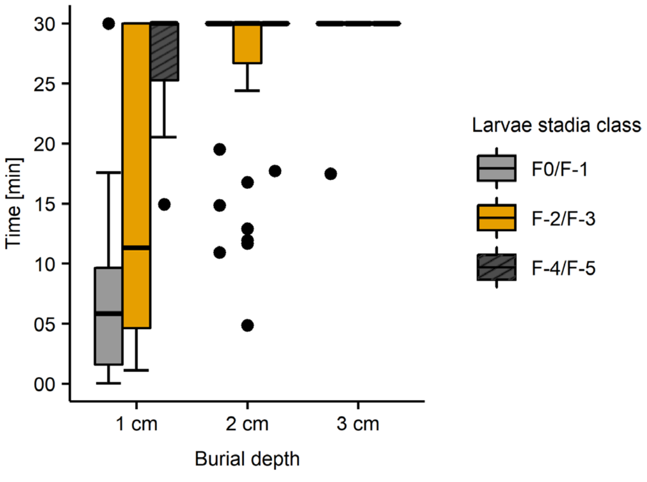

FIGURE 3 | Time measurement until first signs at the surface (head/caudal lamellae appearance). On the abscissa, the three burial depths are plotted with the measured time on the ordinate. F0/F-1 and F-2/F-3 are comparable to each other with the same number of individuals ($n=30$), whereas for F-4/F-5 there were only a few larvae available ($n=7$), indicated by a pattern. A tendency of increasing time with lower stadia could be observed. [Color figure can be viewed at wileyonlinelibrary.com]

The majority of *C. mercuriale* larvae were able to excavate themselves at a burial depth of 1 cm. For larvae stadia F0/F-1, 24 out of 30 larvae excavated themselves. Larvae of stadia F-2/F-3 excavated themselves in 18 out of 30 cases. Stadia F-4/F-5 was not comparable to the other two larvae stadia since the number of individuals used in this experiment differed due to their availability; however, 2 out of 7 larvae did excavate themselves. At a burial depth of 2 cm, only a minority of larvae (F0/F-1: 3 larvae; F-2/F-3: 8 larvae; F-4/F-5: 1 larva) excavated themselves. Only one larva (F0/F-1) excavated itself at a burial depth of 3 cm.

For burial depths of 2 cm and 3 cm, the lower layer (0–1 cm) was the layer where the majority of the larvae remained (Figure 5). Larvae numbers were similar in the lower layer for both burial depths. However, fewer larvae were able to excavate themselves at a burial depth of 3 cm (Figures 3 and 4). In addition, one larva appeared in the upper layer (2–3 cm) which was not available for a burial depth of 2 cm. There was no significant difference between the stadia and the layer where the larvae remained for burial depths of 2 and 3 cm.

3.3 | Thanatosis

Thanatosis is a behavior which is expressed through body stiffness in *C. mercuriale* larvae. Legs were mostly tucked up. Thanatosis in-water lasted significantly less time than thanatosis out-of-water on absorbent paper (Wilcoxon signed rank test, Cliff's Delta ($n=38$); $z=-2.502$, $p=0.01236$, $d=-0.36$) (Figure 6). Duration ranged from a few seconds to 07:30 [mm:ss], longer only very occasionally. The mean time for the thanatosis experiment in-water was $m=$02:09 min (median = 00:55 min); the mean time for the thanatosis experiment out-of-water on absorbent paper was $m=$03:29 min (median = 02:01 min).

In experiment (iii), the simulated fish attack did not trigger thanatosis. The majority of the larvae did not show any reactions

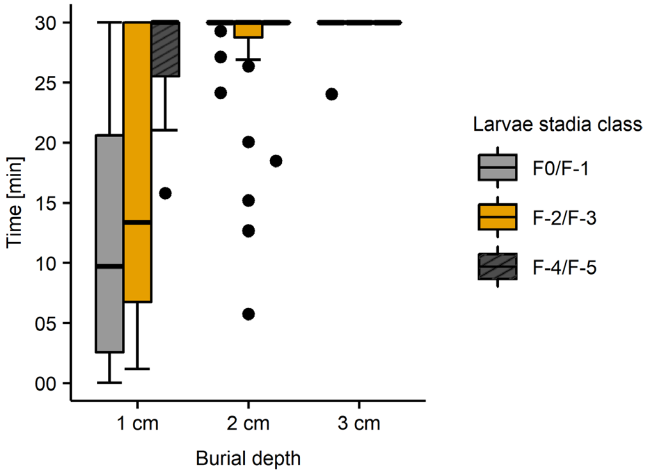

FIGURE 4 | Time measurement until full excavation (body appearance). On the abscissa, the three burial depths are plotted with the measured time on the ordinate. F0/F-1 and F-2/F-3 are comparable to each other with the same number of individuals ($n=30$), whereas for F-4/F-5 there were only a few larvae available ($n=7$), indicated by a pattern. A tendency of increasing time with lower stadia could be observed. [Color figure can be viewed at wileyonlinelibrary.com]

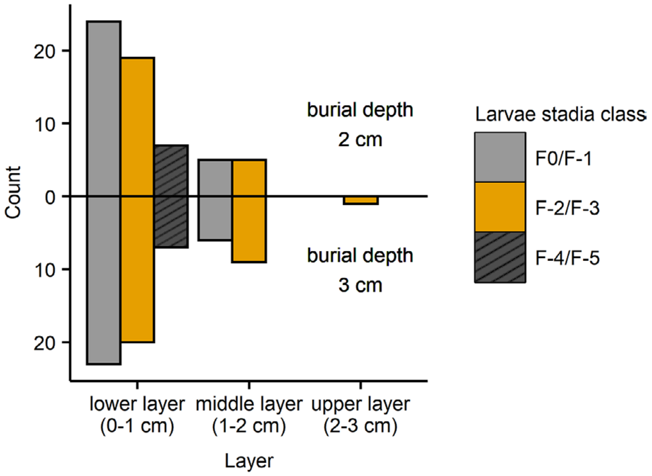

FIGURE 5 | Layer where the larvae remained for two burial depths (2 cm and 3 cm). After 30 min, the layer in both depths was the lower layer (0–1 cm) for the majority. Larvae of stadia F-4/F-5 are patterned due to the disparate number of larvae used during the experiment. [Color figure can be viewed at wileyonlinelibrary.com]

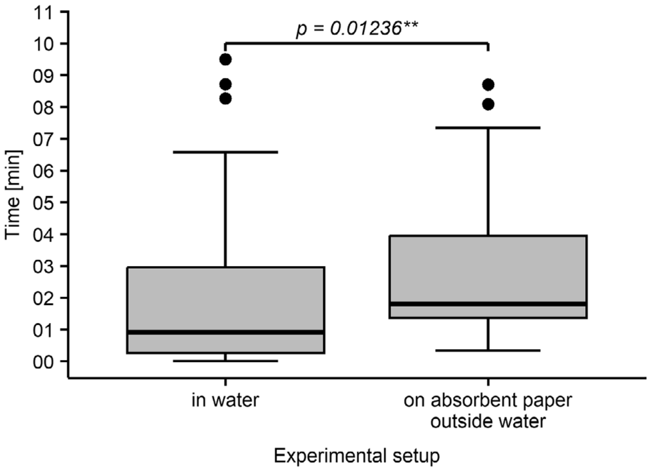

FIGURE 6 | Thanatosis: water vs. absorbent paper out-of-water. The length of time differed between the two experiments with increasing time by placing the larvae on absorbent paper out-of-water.

($n = 32$); some ($n = 6$) did show swimming movements and left the site. In additional experiments with five larvae, habitat management activities were simulated to test if they induce thanatosis as well. Jiggling and cutting the hosting aquatic plant with a pruner to simulate a mowing bucket resulted in thanatosis ($n = 3$), swimming away ($n = 1$), or holding onto the cut stem ($n = 1$).

4 | Discussion

4.1 | Habitat Choice

The present study showed a preference for aquatic plants with broad leaves and a stable stem by the Zygoptera larvae *C. mercuriale*; here *Phragmites australis* and *Veronica beccabunga*. This is in contrast to Krecker (1939), who identified that aquatic plants with entire, ‘ribbon-like’ leaves have a smaller and less varied animal population than plants with subdivided or curled leaves. In a few cases, *C. mercuriale* larvae were found in the leaves or floating roots of *V. beccabunga*. In the field, plants with soft stems like *V. beccabunga* and *Glyceria fluitans* are preferred for oviposition by *C. mercuriale* females (Buchwald 1989). Additionally, the field experiment by Thelen (1992) supports our results, where the highest number of *C. mercuriale* larvae occurred in *N. officinale*, a plant species with a comparable structure to *V. beccabunga*. Harrod (1964) explains different preferences for different aquatic plant species within an order (for Zygoptera: suborder) by the locomotion habits of species. More active predators show a universal distribution on all available plant surfaces, whereas less active predators hardly leave and stay on their preferred plant (Harrod 1964). During our experiment, the larvae seldom left the preferred aquatic plant that they chose in the first place. That outcome matches the field work results of Thelen (1992), who hypothesized that the larvae seldom leave the aquatic plant habitat after hatching.

Even when previous studies show preferences for soft stem plants by *C. mercuriale*, larvae might stay where they hatch, even if oviposition has been in *Callitriche* spp. or *Elodea canadensis*. In our experiment, larvae also occurred in those two macrophytes which are known for oviposition (Sternberg and Buchwald 1999) and, in the case of *E. canadensis*, for Zygoptera larvae as well (Krecker 1939). Our somewhat ambiguous experimental outcome is supported by the study of Cyr and Downing (1988), which stated that leaf structure is not the only factor influencing total invertebrate abundance.

4.2 | Sediment Burial

4.2.1 | Time Duration

Up to this point, no preceding studies about response behavior to burial by Zygoptera larvae are known to the authors of the present study. These larvae seem to be more tolerant to fine sediment burial since they can excavate themselves to greater burial depths than EPT (Wood et al. 2005). However, tolerance through excavating decreases strongly with greater sedimentation levels. For a burial depth of 3 cm, only one larva of stadia F0/F-1 managed to excavate. Differences in tolerance through excavating from sediment burial can be inter-order (Wood et al. 2005) but also intra-order (Conroy et al. 2018), especially for different sediment size classes. Wood et al. (2001) analyzed that larvae of a caddisfly were able to excavate faster from coarser sediment than from finer sediment. During habitat management in ditches and streams, finer sediment more frequently induces a higher impact and lowers oxygen availability.

A tendency of increasing time duration of excavation was observed with smaller larval stages. This has also been observed by Wood et al. (2001). Individuals of the last and second last stadia had significantly greater success in excavation regarding the first signs of appearance than smaller larval stadia. In addition, with increasing burial depth, a tendency of increasing time duration for appearance was observed, as has already been observed by Conroy et al. (2018). Interestingly, the time distribution is greater for body appearance than for head/caudal lamellae for larval stadia F0/F-1. Mean time duration increased for both stadia F0/F-1 and F-2/F-3 for 1 cm between head/caudal lamellae and body appearance. A longer lag between head and body appearance has also been reported for two trichopteran species, which might be caused by body structure (Conroy et al. 2018). In addition, a broad distribution concerning burial depths is possible due to different individual reactions. Some larvae might not try to excavate themselves, especially since Zygoptera were not known yet for their excavating methods.

4.2.2 | Layer Where the Larvae Remained

It is possible that the larvae would have excavated themselves after the 30 min duration of the experiment. In addition, the excavation possibility might be greater for larvae to remain in deeper layers after 30 min. However, *C. mercuriale* is a threatened damselfly, protected under the Habitats Directive, so the authors aimed to prevent the risk of death due to lacking oxygen supply with increasing time duration.

A similar number of stadia F0/F-1 and F-2/F-3 larvae remained in the same layer for burial depths of 2 cm and 3 cm, so that no greater success in reaching a deeper layer could be observed within these two stadia classes. However, deeper layers have been reached by more F-2/F-3 larvae for a burial depth of 3 cm. This could be associated with different reactions by individuals, whereby some larvae might not try to excavate themselves.

4.3 | Thanatosis

In addition to other Odonata larvae, *C. mercuriale* larvae display thanatosis. The time duration between thanatosis in-water and out-of-water on absorbent paper differed significantly, as previously described by Wildermuth (2000). According to Henrikson (1988), thanatosis is a typical anti-predator reaction for Odonata exposed to fish in their habitat. The waterbodies of the *C. mercuriale* larvae used in our experiments contained fish as well. However, additional experiments showed that larvae moved around the stem while grabbing it. Simulated fish attacks did not trigger any thanatosis, so that only successful predation attacks might trigger thanatosis (Wildermuth 2000). This would induce losing interest for non-moving *C. mercuriale* larvae. Triggered thanatosis in-water can increase drift when larvae live in microhabitats exposed to the current (see also Otto and Sjöström 1983). Drift increases the risk of transport to unfavorable sites (Otto and Sjöström 1986) and can decrease the survival rate (Otto and Sjöström 1983). However, drift risk might be low when entering thanatosis because *C. mercuriale* larvae are known to live in weaker current areas (Rouquette and Thompson 2005).

4.4 | Consequences for Habitat Management of Waterbodies

Our results lead to conflicts in habitat management of small lotic waterbodies. On the one hand, the consideration of microhabitats, in this case the vegetation, could be in conflict with flood management and the preservation of flow, which is of relevance for habitat management (Idilbi et al. 2024; Bączyk et al. 2018). On the other hand, removal of aquatic plants maintains habitat quality by preventing overgrowth, which would then decrease habitat suitability until the disappearance of *C. mercuriale*. In addition, the management of invasive macrophytes has to be considered. Selective invasive aquatic plant control for the restoration of native diversity does not affect macroinvertebrates severely (Kovalenko et al. 2010). Invasive non-native species as possible habitat for threatened macroinvertebrate species should still be considered as the habitat choice experiment shows. If the complete removal of an invasive alien plant in terms of eradication is no longer possible, one could preferably leave parts unmanaged or with adapted management for macroinvertebrates. Eventually, both the removal of macrophytes in habitat management activities and (for waterbodies with overgrowth risk) no habitat management constitute a degradation of the habitat and a loss of macroinvertebrate biomass and diversity.

In addition, the pressure of vegetation removal, habitat degradation, and sedimentation increases with dredging activities (Essink 1999), which can also be induced by mowing buckets through obstructed sight or restricted hydraulic possibilities of swiveling. Therefore, threats are posed to sediment deposition during habitat management since burial depths starting from 2 cm are already difficult to manage through excavating by *C. mercuriale* larvae and other macroinvertebrates such as trichopteran larvae (Dobson et al. 2000). In addition, macroinvertebrate drift can increase with sediment load (Rosenberg and Wiens 1978). Furthermore, smaller larval stages seem to be more vulnerable to burial than larger ones (Wood et al. 2001), matching our results for excavating success by smaller larval stages of *C. mercuriale*. This indicates that habitat management should preferably not be performed too close to the hatching period of *C. mercuriale* larvae, which is about a month after oviposition (Corbet 1957) between June and August (Wildermuth and Martens 2019). Nevertheless, the time for habitat management should be before November, especially for poikilothermic Odonata larvae. The colder water temperatures result in less mobility of Odonata, leading to less excavation (Tobias 1995).

Another pressure from habitat management is thanatosis. The habitat management simulation experiment revealed that thanatosis in *C. mercuriale* larvae is induced by habitat management and therefore could decrease the survival rate due to increased predation risk through drift (see Otto and Sjöström 1983). Out-of-water, thanatosis was triggered and endured longer than in water. Dawson et al. (1991) indicated that a high number of macroinvertebrates are removed with cut weed. This might increase predation risk even more when thanatosis is induced out-of-water and might reduce the successful return to the waterbody of *C. mercuriale* larvae.

5 | Conclusions

Habitat management affects macroinvertebrates in several ways. Our study shows that threatened damselfly larvae of *Coenagrion mercuriale* are not tolerant of deeper fine sediment burial layers. In addition, habitat management can induce thanatosis, which is detrimental in the case of drift and risk of predation. *C. mercuriale* larvae do not show a clear preference for aquatic plants; however, they are affected by removing all kinds of aquatic plants during habitat management. The latter includes the removal of invasive aquatic plant species such as *Elodea canadensis*, since the larvae inhabit most plants as well. Future research could address drift impacts and further field experiments concerning the impacts of habitat management.

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Conflicts of Interest

The authors declare no conflicts of interest.

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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