Survival durations and behavioural adjustments of two freshwater bivalves (*Unio terminalis*, Unionida and *Corbicula fluminea*, Venerida) under two emersion conditions

Mehmet Güler[*]

Aydın Adnan Menderes University, Faculty of Agriculture, Department of Aquaculture and Fisheries, Aydın 09100, Turkey

Abstract – Freshwater bivalves in shallow waters are often exposed to extended periods of drought and are highly affected due to their limited mobility. Their adaptation to emersion is a key factor for survival, particularly during human-made unnatural water regime fluctuations or short-term droughts. In the current study, survival durations of two freshwater bivalve species (*Unio terminalis*, Unionidae and *Corbicula fluminea*, Cyrenidae) were tested under two experimental emersion conditions (presence of water-saturated sediment and without sediment). *U. terminalis'* mean survival duration more than doubled in the water-saturated sediment treatment (992 h) compared to treatment without sediment (448 h). For *C. fluminea*, the mean survival duration in the water-saturated sediment treatment (278 h) was over 50% longer than that recorded in the treatment without sediment (174 h). Both species probably made behavioral adjustments according to the environmental conditions to respond to the presence of the water-saturated sediment and maximized their survival chances. In general, *U. terminalis* survived significantly longer than *C. fluminea* in both treatments. No effects of size on survival were observed for either species.

Keywords: Drought / dewatering / survival / clam / sediment

1 Introduction

Responses of organisms inhabiting freshwater systems to drought are variable, and moving to a more favourable environment is one response that is commonly observed in insects or fishes (Labbe and Fausch, 2000; Magoulick and Kobza, 2003; Lytle *et al.*, 2008). Freshwater bivalves have limited mobility or none at all (Toomey *et al.*, 2002; Newton *et al.*, 2015; Vaughn *et al.*, 2015). In shallow waters, they are often exposed to extended periods of drought (Byrne *et al.*, 1988; Byrne and McMahon, 1994; Vaughn *et al.*, 2015) and are highly affected, mainly in terms of abundance decline and decrease in species diversity (Gagnon *et al.*, 2004; Golladay *et al.*, 2004; Haag and Warren, 2008; Galbraith *et al.*, 2010; Allen *et al.*, 2013; Sousa *et al.*, 2016). Although some species have the capacity to survive drought for extended periods, generally their adaptations do not seem adequate to tolerate human-made unnatural water regime fluctuations or droughts (Bogan, 2008; Haag, 2012; Leuven *et al.*, 2014; Galbraith *et al.*, 2015; Vaughn *et al.*, 2015; Sousa *et al.*, 2016). Assessing bivalve capacity to survive drought is important, especially for water management and conservation applications (Johnson *et al.*, 2001; Collas *et al.*, 2014; Nakano, 2018).

Emersion tolerances of freshwater bivalves can be considered a key adaptation factor for survival, particularly for short-term droughts (Byrne & McMahon, 1994; Nakano, 2018). There are various physiological and morphological characteristics that effect tolerance levels (consequently the probability of survival) of freshwater bivalves that are exposed to drought, such as shell thickness, shell shape or valve closure adjustments (Byrne and McMahon, 1994; Bartsch *et al.*, 2000; Nakano, 2018). Tolerance levels are highly variable and species-specific (Holland, 1991; Mitchell *et al.*, 2018). In the example of unionids, Nakano (2018) reported about 50 h mean survival duration for *Sinanodonta japonica* in an emersion trial, Holland (1991) reported about 150–200 days mean survival time for *Uniomerus tetralasmus*. Even though the experimental setups in these studies were different, variations in survival durations of various species were conspicuously high. Therefore, it seems difficult to make a general estimation on their survival capacities and information on each new species studied would have a remarkable contribution.

The tolerance level of an emersed bivalve can be associated with the moisture level of the environment (Byrne and McMahon, 1994; Nakano, 2018), with temperature (Bartsch *et al.*, 2000; Mitchell *et al.*, 2018) or the presence of sediment

*Corresponding author: mehmetguler@adu.edu.tr

(Gough *et al.*, 2012; Mitchell *et al.*, 2018) as well as its physiological and morphological characteristics (Byrne and McMahon, 1994; Bartsch *et al.*, 2000; Nakano, 2018). The aim of this study was to test the emersion tolerances of two freshwater bivalves *Unio terminalis* (Bourguignat, 1852) and *Corbicula fluminea* (Müller, 1774) in moist sediment during a prolonged drought, using experimental setups with water-saturated sediment. Although some researchers mention the positive effects of reaching the moist sediment or micro sheltered areas (Holland, 1991; Gagnon *et al.*, 2004; Gough *et al.*, 2012; Mitchell *et al.*, 2018), there is no satisfactory information on how it happens. Additionally, a group without-sediment was set up to assess the effects of water-saturated sediment and to make comparisons with previous studies (*e.g.*, Collas *et al.*, 2014; Nakano, 2018; Guareschi and Wood, 2020). The experimental setups were also suitable to evaluate the effects of bivalve sizes; research on size-survival relationships during droughts is surprisingly limited, and only a small number of experimental studies are available (*e.g.*, Byrne *et al.*, 1988; Nakano, 2018).

The species investigated in the study cohabitate in the same area (River Çine, western Turkey). The first species, *U. terminalis*, is a member of the family Unionidae, endemic to the Middle East and according to IUCN Red List, classified as "vulnerable" (Graf and Cummings, 2007; Lopes-Lima and Seddon, 2014). The second, *C. fluminea*, is a well-studied venerid species that is a successful invader throughout the world's inland waters (Sousa *et al.*, 2008; Kamburska *et al.*, 2013; Ferreira-Rodríguez and Pardo, 2016). Interaction between these species was not the subject of the present study, but results may provide an example of how one native and one non-native bivalve cope with drought conditions in different ways.

2 Materials and methods

Both species were collected by hand from the River Çine (western Turkey, 37°45′50.5″N 27°49′59.8″E) in May, 2017; the water temperature was 19.5 °C. Collected bivalves were placed in isolated polystyrene foam boxes and transferred to the laboratory of the aquaculture research facility of ADÜ Faculty of Agriculture, Department of Fisheries and Aquaculture (ADÜ-SAUB). Before the treatments, the specimens were placed in tanks with one transparent side, filled with aerated fresh water (underground water that supplies the facility) at 19 °C and were observed for 24 h. To ensure standardization, only individuals with quick valve responses and foot or siphon movement were included in the treatments. Subsequently, two treatments were performed using both species: (1) treatment without sediment, and (2) water-saturated sediment treatment.

In the first treatment (treatment without sediment), bivalves were dried using blotting paper and placed side by side in dry empty plastic containers (8–10 per container for *U. terminalis*, 7 containers; 15–20 per container for *C. fluminea*, 4 containers). Before the placement of the bivalves, containers were placed in a water canal in the facility in order to obtain the desired level of humidity and temperature; containers were in continuous contact with water throughout the treatments (in a pilot study that was conducted in an air-conditioned room, relative humidity decreased

sharply). The water in the channel was constantly flowing, and temperatures varied between 18 and 20 °C during the treatments. Concrete blocks were placed inside the containers to prevent them from floating or moving.

The second treatment (water-saturated sediment treatment) was conducted in plastic containers (39 × 28 × 19 cm) filled with sediment approximately 15 cm in height. The sediment used in the treatments (sandy loam texture; according to Soil Science Division Staff, 2017) was taken from the area of the river where the bivalves had been collected. Setups were placed in the water canal with constant water flow and the containers were in continuous contact with water, such as the treatment without sediment setup. Bivalves were placed in the containers, 8–10 per container for *U. terminalis* (6 containers) and 12–20 per container for *C. fluminea* (5 containers). Prior to the placement of the bivalves, the containers were filled with water to the upper level of the sediment. Water was given time to penetrate the sediment completely, and the bivalves were placed gently into the sediment by hand; then a few centimetres of water was added. The bivalves rapidly took their natural positions in the sediment. The supernatant water layer and the remaining thin water film was removed by using sponges. Water adjustments were made continuously to prevent the effects of evaporation throughout the experimental period according to this protocol. The sediment in the containers was changed every 10–12 days to prevent deterioration, and the bivalves were placed in the new sediment with the initial sediment characteristics.

Treatments were conducted in the natural photoperiod (indoor, 14–15 h light, 10–9 h twilight and dark). Observations of the setups and recording of the deaths were made twice a day (between 7:30 and 8:30; both am and pm); in some cases, observations could not be made on time, but no deaths occurred in those instances. Stimulation of the mantle edges of the bivalves was used to confirm survival, stable valve opening, and no valve or tissue response were criteria of death (Paukstis *et al.*, 1999; Nakano, 2018) for both treatments. Dead individuals were removed from the setups in both treatments. Data from five *U. terminalis* that were stranded on the sediment surface were excluded from the analyses. The air temperature inside the containers and temperature of the sediment varied between 18 and 21 °C and the relative humidity of the environment was $79 \pm 9\%$ throughout the treatments. All of the individuals were marked with their own death times after their death.

Both species were examined under two size categorize according to their shell lengths (SL, distance between anterior and posterior ends, Tab. 1). The Kaplan-Meier estimator was used to make survival analyses for both species and for each size group for each treatment (Kaplan and Meier, 1958). Survival times were indicated as mean survival time (average of the all death times recorded in the related treatment ± std. error; as hours). For *U. terminalis*, the effects of the treatment conditions (without sediment and water-saturated sediment) and bivalve size (covariate), and their interaction on survival time were tested with a two-factor analysis of variance (ANOVA). Prior to testing, *Ln* transformation was used since the data did not satisfy the assumptions of homogeneity of variance. In *C. fluminea*, the effects of the treatments (without sediment and water-saturated sediment) and the bivalve size (covariate), two factors plus their interaction on survival time

Table 1. Summary of the sizes (mm) and numbers of the individuals used in the experiments.

Species	Treatment	Size	N	Mean	SD
Unio terminalis	Without sediment	Small	23	47.6	9.6
		Large	43	79.4	11.3
	Saturated sediment	Small	25	49.5	9.7
		Large	26	81.4	10.6
Corbicula fluminea	Without sediment	Small	28	18.8	2.7
		Large	45	26.1	1.9
	Saturated sediment	Small	41	19.3	2.3
		Large	42	26.0	1.9

were tested with a generalized linear model (model: main effects of both factors and their interaction; distribution: gamma). Additionally, the overall values (regardless of size) were compared with Mann-Whitney U test to double-check the effects of treatment in case of *C. fluminea*. To compare survival times between *U. terminalis* and *C. fluminea*, survival times for small and large bivalves were pooled for each species (regardless of size), then the Kaplan–Meier estimator was used to determine the survival function, and the Mantel-Cox test (Logrank) was performed. This procedure was used for treatment without sediment and treatment with saturated sediment separately. Statistical analyses were performed with SPSS Statistics, Version 23 (IBM Corp., Armonk, NY, USA).

3 Results

In the treatment without sediment with *U. terminalis*, the mean survival times for the different size classes were found to be 440 ± 18 (mean $\pm$ SE) hours and 452 ± 14 h for the small and large individuals, and the overall value (without size classification) was 448 ± 11 h (Figs. 1 and 2). The survival times did not differ with respect to size (Tab. 2). The survival times in the saturated sediment treatment were 1009 ± 50 and 977 ± 39 h for the small and large size groups, respectively (overall survival time 992 ± 32 h) and did not differ according to size (Figs. 1 and 2, Tab. 2). In this treatment, the survival times were found to be higher than those in the treatment without sediment, and *U. terminalis* survived 121% longer in the sediment than the setup without sediment (Fig. 1, Tab. 2).

In the treatment without sediment, the mean survival times for *C. fluminea* were recorded as 172 ± 4 and 175 ± 3 h, for small and large size groups respectively (Figs. 1 and 2); the overall value was 174 ± 2 h. Survival times did not differ significantly according to size (Tab. 3). The mean survival times in the saturated sediment treatment were 284 ± 18 and 272 ± 17 h for the small and large size groups, and the overall survival time was 278 ± 12 h (Figs. 1 and 2). Size was not a significant predictor of the survival rate (Tab. 3). The survival times in the saturated sediment were 60% higher than in the treatment without sediment (Figs. 1 and 2), differences were significant (Tab. 3). According to the additional test, survival times between two treatments was significantly different (Mann-Whitney $U = 972.5$, $z = 7.37$, $p < 0.01$).

In general, *U. terminalis* survived longer than *C. fluminea* for both without sediment (Mantel-Cox test, $\chi 2 = 153.4$, $df = 1$,
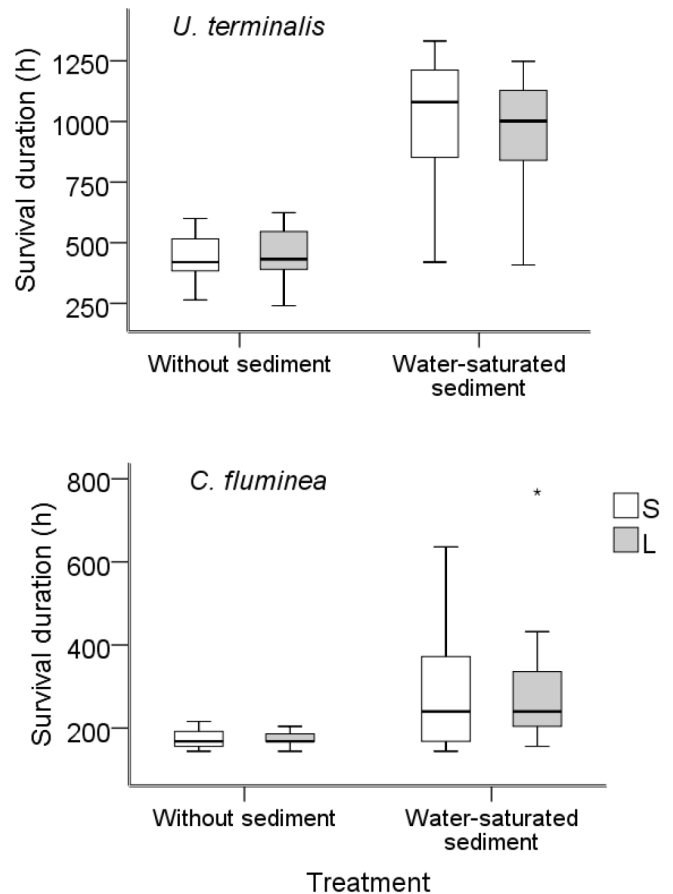

Fig. 1. Survival durations for different sized *U. terminalis* and *C. fluminea* in without sediment and water-saturated sediment treatments. The box plots show median, 25th and 75th quartile, horizontal lines: maximum and minimum, ∗: extreme value.

$p < 0.01$) and saturated sediment (Mantel-Cox test, $\chi 2 = 128.74$, $df = 1$, $p < 0.01$) treatments (Fig. 1).

4 Discussion

In the current study, the mean survival times under without sediment treatment were found to range from 440 to 452 h for small and large *U. terminalis*. The tolerance of some unionid bivalves can extend up to months (*e.g.*, *U. tetralasmus*, Holland, 1991) but shorter survival times are reported frequently (see Collas *et al.*, 2014; Nakano, 2018). For example, the mean survival duration findings of Nakano (2018) on six unionid species (*Nodularia douglasiae biwae*, *Pronodularia japanensis*, *Obovalis omiensis*, *Lanceolaria grayii*, *Inversidens brandtii*, and *Sinanodonta japonica*) varied between 48 and 144 h (71% relative humidity, RH; 25 °C). Collas *et al.* (2014) reported 173 and 183 h LT$_{50}$ (lethal time for 50% mortality) for *U. tumidus* and *Unio pictorum* (68% RH; 20 °C); the temperatures in these studies (Collas *et al.*, 2014; Nakano, 2018) were not too different from those recorded in the present study. For unionids, emersion tolerances and consequently survival durations can be highly variable among different species (see Mitchell *et al.*, 2018) and the present
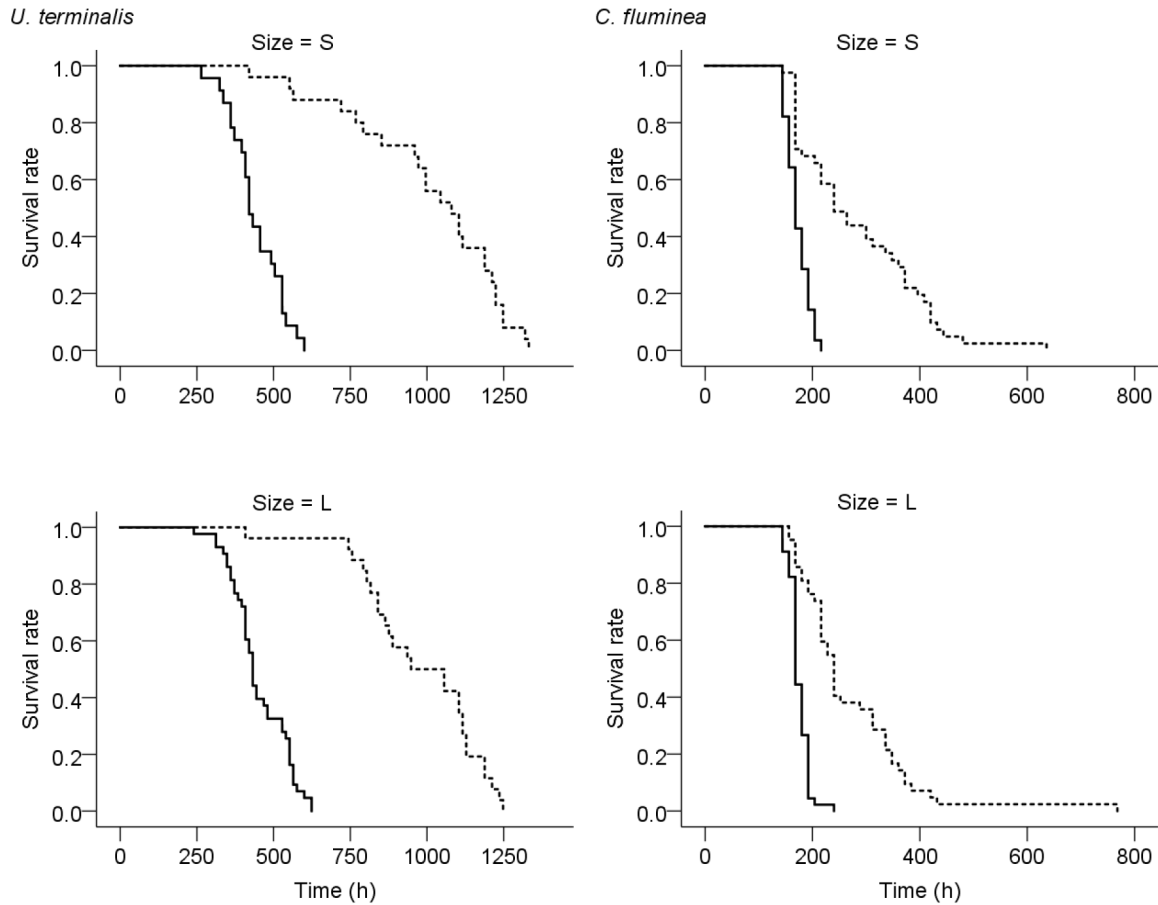
Fig. 2. Survival analyses (Kaplan-Meier survival curves) of different sized *U. terminalis* and *C. fluminea* in without sediment (lines) and water-saturated sediment (dashed lines) treatments over experiment time.

Table 2. Results of the two-factor ANOVA for the effects of treatments (without sediment and saturated sediment conditions) and bivalve size on survival time in *U. terminalis*.

Source	df	Mean Square	F	p
Treatment	1	2.06	36.85	<0.01
Size	1	0.00	0.00	0.97
Treatment × Size	1	0.10	1.76	0.19
Error	113	0.06	–	–

Table 3. Results of the generalized linear model for the effects of treatment (without sediment and saturated sediment) and mussel size on survival time in *C. fluminea*.

	Wald χ^2	df	p
Treatment	5.85	1	0.02
Size	0.42	1	0.52
Treatment × Size	0.40	1	0.53

study constitutes a new example in this spectrum with the results of *U. terminalis*. For *C. fluminea*, Collas *et al.* (2014) found an LT_{50} of 224 h (68% RH; 20 °C). Guareschi and Wood (2020) reported shorter LT_{50} at the same temperature (55 h, 81% RH; 20 °C), and they stated that the differences between findings of Collas *et al.* (2014) may be caused by factors such as experimental design, acclimation periods and humidity values. Byrne *et al.* (1988) found 73–78 h at 25 °C and 253–342 h at 15 °C (in various RH). They also stated that the effects of humidity on survival times of this species were less important than temperature; temperature has also been reported as one of the primary factors affecting the speed of this species' spread across the world (Crespo *et al.*, 2015).

In the current study, the overall (regardless of size) mean survival time under without sediment treatment for *C. fluminea* was 174 h. The differences of survival durations between previous studies and the present study can be explained by temperature differences, experimental designs and conditions of the animals, which might affect the regularity functions in bivalves (Taylor and Brand, 1975). It should also be noted that different calculating methods (*e.g.* mean survival, LT_{50}) may have an effect on the results.

As one of the main results of the current study, it was found that water-saturated sediment provides protection and more than doubles the survival times for *U. terminalis*. To explain this situation, the general information on the adaptations of

the bivalves to emersion may be reconsidered taking into account some behavioural patterns observed during the treatments in this study. In marine bivalves, some species close their valves tightly and remain anaerobic when emersed, and some of them gape their valves so that their tissues come into direct contact with air (Boyden, 1972; Widdows *et al.*, 1979; McMahon, 1988; Sadok *et al.*, 1999; Hicks and McMahon, 2003). The second adaptation can be considered more effective, but tissue desiccation is the limiting factor (McMahon, 1988; Hicks and McMahon, 2003; Nicastro *et al.*, 2010), and general metabolism is affected in both adaptations (Coleman, 1973; McMahon, 1988; Shick *et al.*, 1988). Freshwater bivalves have somewhat different and more effective adaptations. Many unionid bivalves periodically gape; some of them seal the mantle edges with mucus so that their tissues are not directly exposed and moisture loss is kept to minimum levels, or in some cases, they switch from aerobic to anaerobic respiration (Holland, 1991; Byrne and McMahon, 1994; McMahon and Bogan, 2001). Relatively longer survival times recorded with *U. terminalis* in the current study may be explained by the aforementioned adaptations, but only for the treatment without sediment. In the water saturated sediment treatment, *U. terminalis* left their valves slightly (or more) open while maintaining their position with part of their body below the sediment. This may mean more air contact than in the sealed mode, and still guarantees minimum moisture loss and prevents tissue desiccation due to continuous contact with water, thus leading to longer survival times. One of the primary factors of the survival limitation is the osmotic concentration (osmolarity) of the body fluids (Dietz, 1974). With this behaviour, *U. terminalis* may efficiently balance O_2 demands and moisture retention, which are considered to be the main aspects of emersion tolerance (McMahon, 1988; Byrne and McMahon, 1994). Moreover, anaerobic conditions and prolonged valve closure may lead to the accumulation of metabolism endpoint products (Widdows *et al.*, 1979; Byrne *et al.*, 1988; McMahon, 1988; Byrne *et al.*, 1990). If tissues come into contact with the water under the sediment (it could be observed in the current research), this behaviour could reduce the effects of the accumulation of metabolic endpoint products; however, further research is required. As a result, it can be suggested that unionids in the present study shifted and/ or mixed their adaptation modes in response to two different drought patterns that can occur in the field and maximized their survival chances by using the suitable mode.

In the current study with *C. fluminea*, saturated sediment provided protection from desiccation as well, and made survival times longer; however, this observation should be evaluated in a different way from *U. terminalis* because of the possibility of the existence of different types of adaptation. When emersed, *C. fluminea* can consume O_2 across the protruded mantle edge tissues (sealed together with hardened mucus under low humidity) or remain with closed valves until the external conditions are restored (McMahon and Williams, 1984; Byrne *et al.*, 1988; McMahon, 1988; Byrne *et al.*, 1990). These suggestions may be compatible with the observations made on the valve closure behaviours of *C. fluminea* during the treatment without sediment. In the water saturated sediment treatment, most of the clams located themselves under the sediment and positioned under or near miniature pools formed by their movements (see Supplementary Fig. S1).

Some of these "pools" were covered with sediment, some of them were not. As far as it could be observed, their tissues were in contact with these miniature structures (if formed) or at least in contact with the water-saturated sediment. This behaviour may have a similar effect on O_2 demands and moisture retention balance as mentioned in the previous paragraph. Therefore, different modes were observed in *C. fluminea* for different environments. This result may support the theories on the ability of this species to make behavioural adjustments to adapt to environmental conditions (Byrne *et al.*, 1988), as well as unionids (Allen and Vaughn, 2009; Gough *et al.*, 2012; Chmist *et al.*, 2019), and may provide evidence to support the suggestions on the possible positive effects of moist sediment on survival (Holland, 1991; Gough *et al.*, 2012; Collas *et al.*, 2014; Mitchell *et al.*, 2018). Generally, the survival times of *C. fluminea* increased when exposed to saturated sediment, but not as much as those observed in *U. terminalis*, and this behaviour was not as effective as it was for unionids. It should be noted that the described behaviours for both species during the treatments were not entirely continuous and, most importantly, the water-saturation levels in the field do not remain constant. Additionally, it is possible that the different environmental conditions (absence or presence of the sediment) may have created different levels of stress on the bivalves during the treatments. Although it is a natural part of the overall effect, stress can be considered as an additional factor to the aforementioned effects.

Although some studies suggest that shell size is a predictor of emersion tolerances of freshwater bivalves, the relationship between size and survival is not completely clear, especially in unionids. Sousa *et al.* (2018) suggested that the smaller *Margaritifera margaritifera* (Linnaeus, 1758) are more susceptible to die-offs during droughts, but differences were significant for only the specimens from one river among three rivers (North West of the Iberian Peninsula). Collas *et al.* (2014) reported that the LT_{50} values increased significantly with increasing shell length but that study had a multiple species approach. In another experimental study, Nakano (2018) reported that the unionid species that had longer shells and greater masses had longer survival times for two of a total of six species studied. Additionally, Nakano (2018) found longer survival times for lighter species but not for all species and not in all analyses. According to Bartsch *et al.* (2000) emersion sensitivity may decrease with increasing mussel size due to decreasing surface area to volume ratio and thicker shells may increase emersion tolerances. In another study with *C. fluminea*, no significant effect of size on emersion tolerance was found (Guareschi and Wood, 2020).

In the current study, the survival durations did not differ in accordance with bivalve size for either species, and in both environmental setups, and no evidence was found to suggest that size (within species) had any effect on emersion tolerances. However, the function of size should be further studied for different species in wide size ranges, as well as other morphological features, and should be supported by field studies. A better understanding of the possibly more sensitive sizes and therefore life phases of these animals (especially threatened species) can provide important information for conservation efforts. Additionally, knowledge of survival capacities during drought may be used in determining

the spreading dynamics of *C. fluminea* and help management studies on preventing the further spread of this invasive species. The effects of moist sediment, which was found to be significant in the present study, can be further examined in experimental/controlled conditions, focusing on the physiological mechanisms of the bivalves to provide a better understanding of the function of moist sediment during drought.

The results of the study may answer some questions that can arise during field studies on the size distribution and population structures of freshwater bivalves, as well as questions on the effects of moist sediment in dewatered areas. Tolerance results can also be used on a wider scale. Culture studies for *C. fluminea* still continue (Chang *et al.*, 2017; Serdar, 2018), and aquaculture for unionids has been a subject of study for at least a century (see Gatenby *et al.*, 1996; Barnhart, 2006; Douda, 2015). Knowledge of the tolerance to emersion and the effects of habitat features such as sediment may be used in mussel transfer, stock enhancement or aquaculture studies on these animals. In general, it is clear that the tolerance levels of different freshwater bivalve species can be highly variable and that different tolerance levels of species living in the same area should be taken into account in water management efforts.

Supplementary Material

Supplementary Figure S1. Water saturated sediment treatment; miniature pools formed by the movements of large sized *C. fluminea*.

The Supplementary Material is available at https://doi.org/10.1051/limn/2020027.

References

Allen DC, Vaughn CC. 2009. Burrowing behavior of freshwater mussels in experimentally manipulated communities. *J N Am Benthol Soc* 28: 93–100.

Allen DC, Galbraith HS, Vaughn CC, Spooner DE. 2013. A tale of two rivers: Implications of water management practices for mussel biodiversity outcomes during droughts. *Ambio* 42: 881–891.

Barnhart MC. 2006. Buckets of muckets: a compact system for rearing juvenile freshwater mussels. *Aquaculture* 254: 227–233.

Bartsch MR, Waller DL, Cope WG, Gutreuter S. 2000. Emersion and thermal tolerances of three species of unionid mussels: survival and behavioral effects. *J Shellfish Res* 19: 233–240.

Bogan AE. 2008. Global diversity of freshwater mussels (Mollusca, Bivalvia) in freshwater. *Hydrobiologia* 595: 139–147.

Boyden C. 1972. The behaviour, survival and respiration of the cockles *Cerastoderma Edule* and *C. Glaucum* in air. *Mar Biol Assoc U.K.* 52: 661–680.

Byrne RA, McMahon RF. 1994. Behavioral and physiological responses to emersion in freshwater bivalves. *Amer Zool* 34: 194–204.

Byrne R, McMahon RF, Dietz TH. 1988. Temperature and relative-humidity effects on aerial exposure tolerance in the fresh-water bivalve *Corbicula fluminea*. *Biol Bull* 175: 253–260.

Byrne R, Gnaiger R, Mcmahon R, Dietz T. 1990. Behavioral and metabolic responses to emersion and subsequent reimmersion in the freshwater bivalve *Corbicula fluminea*. *Biol Bull* 178: 251–259.

Chang P, Chang W, Shih C, Liu D, Lee Y. 2017. A study of the growth and burrowing ability for the environmentally friendly cultured freshwater clam *Corbicula fluminea*. *Aquac Res* 48: 3004–3012.

Chmist J, Szoszkiewicz K, Drożdżyński D. 2019. Behavioural responses of *Unio tumidus* freshwater mussels to pesticide contamination. *Arch Environ Contam Toxicol* 77: 432–442.

Coleman N. 1973. The oxygen consumption of *Mytilus edulis* in air. *Comp Biochem Physiol Part A Mol Integr Physiol* 45: 393–402.

Collas FP, Koopman KR, Hendriks AJ, van der Velde G, Verbrugge LN. Leuven RS. 2014. Effects of desiccation on native and non-native molluscs in rivers. *Freshw Biol* 59: 41–55.

Crespo D, Dolbeth M, Leston S *et al.* 2015. Distribution of *Corbicula fluminea* (Müller, 1774) in the invaded range: a geographic approach with notes on species traits variability. *Biol Invasions* 17: 2087–2101.

Dietz T. 1974. Body fluid composition and aerial oxygen consumption in the freshwater mussel, *Ligumia subrostrata* (Say): effects of dehydration and anoxic stress. *Biol Bull* 147: 560–572.

Douda K. 2015. Host-dependent vitality of juvenile freshwater mussels: implications for breeding programs and host evaluation. *Aquaculture* 445: 5–10.

Ferreira-Rodríguez N, Pardo I. 2016. An experimental approach to assess *Corbicula fluminea* (Müller, 1774) resistance to osmotic stress in estuarine habitats. *Estuar Coast Shelf Sci.* 176: 110–116.

Gagnon PM, Golladay SW, Michener WK, Freeman MC. 2004. Drought responses of freshwater mussels (Unionidae) in coastal plain tributaries of the Flint River basin, Georgia. *J Freshw Ecol* 19: 667–679.

Galbraith HS, Spooner DE, Vaughn CC. 2010. Synergistic effects of regional climate patterns and local water management on freshwater mussel communities. *Biol Conserv* 143: 1175–1183.

Galbraith HS, Blakeslee CJ, Lellis WA. 2015. Behavioral responses of freshwater mussels to experimental dewatering. *Freshw Sci* 34: 42–52.

Gatenby CM, Neves RJ, Parker BC. 1996. Influence of sediment and algal food on cultured juvenile freshwater mussels. *J North Am Benthol Soc* 15: 597–609.

Golladay SW, Gagnon P, Kearns M, Battle JM, Hicks DW. 2004. Response of freshwater mussel assemblages (Bivalvia: Unionidae) to a record drought in the Gulf Coastal Plain of southwestern Georgia. *J North Am Benthol Soc* 23: 494–506.

Gough HM, Gascho Landis AM, Stoeckel JA. 2012. Behaviour and physiology are linked in the responses of freshwater mussels to drought. *Freshw Biol* 57: 2356–2366.

Graf DL, Cummings KS. 2007. Review of the systematics and global diversity of freshwater mussel species (Bivalvia: Unionoida). *J Molluscan Stud* 73: 291–314.

Guareschi S, Wood PJ. 2020. Exploring the desiccation tolerance of the invasive bivalve *Corbicula fluminea* (Müller 1774) at different temperatures. *Biol Invasions* 22: 2813–2824.

Haag WR. 2012. North American Freshwater Mussels: Ecology, Natural History and Conservation. Cambridge: Cambridge University Press.

Haag WR, Warren ML. 2008. Effects of severe drought on freshwater mussel assemblages. *Trans Am Fish Soc* 137: 1165–1178.

Hicks DW, McMahon RF. 2003. Temperature and relative humidity effects on water loss and emersion tolerance of *Perna perna* (L.) (Bivalvia: Mytilidae) from the Gulf of Mexico. *Bull Mar Sci* 72: 135–150.

Holland DF. 1991. Prolonged emersion tolerance in freshwater mussels (Bivalvia: Unionidae): interspecific comparison of behavioral strategies and water loss rates. Master's thesis, University of Texas at Arlington.

Johnson PM, Liner AE, Golladay SW, Michener WK. 2001. Effects of drought on freshwater mussels and instream habitat in Coastal Plain tributaries of the Flint River, southwest Georgia (July–October, 2000). Nature Conservancy, Apalachicola, Florida.

Kamburska L, Lauceri R, Beltrami M, Boggero A, Cardeccia A, Guarneri I, Riccardi N. 2013. Establishment of *Corbicula fluminea* (OF Müller, 1774) in Lake Maggiore: a spatial approach to trace the invasion dynamics. *BioInvasions Rec* 2: 105–117.

Kaplan EL, Meier P. 1958. Nonparametric estimation from incomplete observations. *J Am Stat Assoc* 53: 457–481.

Labbe TR, Fausch KD. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. *Ecol Appl* 10: 1774–1791.

Leuven RSEW, Collas FPL, Koopman KR, Matthews J, Van der Velde G. 2014. Mass mortality of invasive zebra and quagga mussels by desiccation during severe winter conditions. *Aquat Invasions* 9: 243–252.

Lopes-Lima M, Seddon MB. 2014. *Unio terminalis*. The IUCN Red List of Threatened Species 2014: e.T164866A42466771 (accessed October 6, 2020)

Lytle DA, Olden JD, McMullen LE. 2008. Drought-escape behaviors of aquatic insects may be adaptations to highly variable flow regimes characteristic of desert rivers. *Southwestern Nat* 53: 399–402.

Magoulick DD, Kobza RM. 2003. The role of refugia for fishes during drought: a review and synthesis. *Freshwater Biol* 48: 1186–1198.

McMahon RF. 1988. Respiratory response to periodic emergence in intertidal molluscs. *Am Zool* 28: 97–114.

McMahon RF, Williams CJ. 1984. A unique respiratory adaptation to emersion in the introduced asian freshwater clam *Corbicula* Fluminea (Müller) (Lamellibranchia: Corbiculacea), *Physiol Zool* 57: 274–279.

McMahon RF, Bogan AE. 2001. Mollusca: Bivalvia. In: Thorpe J.H. and Covich A.P. (eds.), Ecology and Classification of North American Freshwater Invertebrates, 2nd edn. Academic Press, pp. 331–429.

Mitchell ZA, McGuire J, Abel J, Hernandez BA, Schwalb AN. 2018. Move on or take the heat: can life history strategies of freshwater mussels predict their physiological and behavioural responses to drought and dewatering? *Freshwater Biol* 63: 1579–1591.

Nakano M. 2018. Survival duration of six unionid mussel species under experimental emersion. *Hydrobiologia* 809: 111–120.

Newton TJ, Zigler SJ, Gray BR. 2015. Mortality, movement and behaviour of native mussels during a planned water-level drawdown in the Upper Mississippi River. *Freshwater Biol* 60: 1–15.

Nicastro KR, Zardi GI, McQuaid CD, Stephens L, Radloff S, Blatch GL. 2010. The role of gaping behaviour in habitat partitioning between coexisting intertidal mussels. *BMC Ecol*. 10: 17.

Paukstis GL, Tucker JK, Bronikowski AM, Janzen FJ. 1999. Survivorship of aerially exposed zebra mussels (*Dreissena polymorpha*) under laboratory conditions. *J Freshw Ecol* 14: 511–517.

Sadok S, Uglow RF, Haswell SJ. 1999. Some aspects of nitrogen metabolism in *Mytilus edulis*: effects of aerial exposure. *Mar Biol* 135: 297–305.

Serdar S. 2018. Growth of the Asian clam *Corbicula fluminea* (Müller, 1774) cultured in çine creek, Aydin, Turkey. *J Shellfish Res* 37: 491–496.

Shick JM, Widdows J, Gnaiger E. 1988. Calorimetric studies of behavior, metabolism and energetics of sessile intertidal animals. *Amer Zool* 28: 161–181.

Soil Science Division Staff. 2017. Soil survey manual. In: Ditzler C, Scheffe K, and Monger H.C. (eds.), USDA Handbook 18. Washington, D.C.: Government Printing Office, p. 125.

Sousa R, Antunes C, Guilhermino L. 2008. Ecology of the invasive Asian clam *Corbicula fluminea* (Müller, 1774) in aquatic ecosystems: an overview. *Ann Limnol Int J Lim* 44: 85–94.

Sousa R, Varandas S, Teixeira A, Ghamizi M, Froufe E, Lopes-Lima M. 2016. Pearl mussels (*Margaritifera marocana*) in Morocco: conservation status of the rarest bivalve in African fresh waters. *Sci Total Environ* 547: 405–412.

Sousa R, Ferreira A, Carvalho F, Lopes-Lima M, Varandas S, Teixeira A. 2018. Die-offs of the endangered pearl mussel *Margaritifera margaritifera* during an extreme drought. *Aquat Conserv* 28: 1244–1248.

Taylor AC, Brand AR. 1975. Effects of hypoxia and body size on the oxygen consumption of the bivalve *Arctica islandica* (L.). *J Exp Mar Biol* 19: 187–196.

Toomey MB, McCabe D, Marsden JE. 2002. Factors affecting the movement of adult zebra mussels (*Dreissena polymorpha*). *J North Am Benthol Soc* 21: 468–475.

Vaughn CC, Atkinson CL, Julian JP. 2015. Drought-induced changes in flow regimes lead to long-term losses in mussel-provided ecosystem services. *Ecol Evol* 5: 1291–1305.

Widdows J, Bayne BL, Livingstone DR, Newell RIE, Donkin P. 1979. Physiological and biochemical responses of bivalve mollusks to exposure to air. *Comp Biochem Phys A* 62: 301–308.