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Differences in desiccation tolerance of two Australian freshwater mussel species with different life history characteristics is temperature dependent

Daniel W. Wright · Jason D. Thiem · Elka Blackman · Stephen J. Beatty · Alan J. Lymbery · Sam Davis

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Abstract Mass die-offs, reduced species richness and local extinctions of freshwater mussels have resulted from river drying events, which often co-occur with high ambient temperatures. These events are predicted to increase in frequency and severity under the influence of climate change. We aimed to identify the desiccation tolerance of two freshwater mussel species (the river mussel *Alathyria jacksoni* and the floodplain mussel *Velesunio ambiguus*) across a range of temperatures by simulating river drying events in laboratory conditions. Freshwater mussels were buried in sediment heated to 29, 32, 35, 38 and 41°C. Lethal times and lethal temperatures at which 50% mortality occurred were used to infer species-specific tolerances. The lethal time for 50% of mussels to reach mortality at 29°C was shorter for *A. jacksoni* (14 days) than *V. ambiguus* (58 days) but did not differ markedly at higher temperatures. Lethal temperatures were also similar between species over short durations (e.g. 39–40°C at 1 day). Our results suggest that the difference in desiccation tolerance between species diminishes toward their upper thermal limit. Management interventions aimed at reducing sediment temperatures, such as providing shade via riparian vegetation and wetting from environmental flows, could help alleviate the impact of drying events and climate change on both freshwater mussel species.

Keywords Unionida · Climate change · Drought · Heat · Murray–Darling Basin

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D. W. Wright · J. D. Thiem · E. Blackman
Department of Primary Industries, Narrandera Fisheries Centre, PO Box 182, Narrandera, NSW 2700, Australia

Present Address:
D. W. Wright (✉)
Department of Agriculture, Fisheries and Forestry, Australian Bureau of Agricultural and Resource Economics and Sciences, 70 Northbourne Avenue, Canberra, ACT 2601, Australia
e-mail: daniel.wright@aff.gov.au

S. J. Beatty · A. J. Lymbery
Centre for Sustainable Aquatic Ecosystems, Harry Butler Institute, Murdoch University, 90 South St, Murdoch, WA 6150, Australia

S. Davis
Department of Primary Industries, 37 Carrington Avenue, Dubbo, NSW 2830, Australia

Introduction

Freshwater mussels (Order Unionida) are a diverse group of bivalves, consisting of 958 species (Graf & Cummings, 2021). They provide a range of services that make them important functional components of aquatic ecosystems including water filtration, nutrient cycling and storage, as well as food and habitat for other biota (Vaughn, 2018). In many parts of the world, freshwater mussels also hold cultural significance for indigenous communities, providing spiritual connections to freshwater (Noble et al., 2016). However, freshwater mussels are amongst the most threatened faunal groups with 6% of species considered extinct and a further 32% critically endangered, endangered or vulnerable (IUCN, 2021). There are several threatening processes that impact freshwater mussel populations, most notably pollution, natural system modifications, urban development, exploitation, agriculture, extreme weather events and climate change (Modesto et al., 2018). Their vulnerability to these disturbances is exacerbated by life history characteristics, including their sedentary adult life-phase, dependence on vertebrate species to complete their parasitic life-phase (Modesto et al., 2018), and often their long generation times that slow population recovery (Haag, 2012; Benson et al., 2018, 2019).

Freshwater mussels in Mediterranean regions (regions characterised by hot and dry summers followed by cool and wet winters) are twice as likely to be considered imperilled than those in other parts of the world (Benson et al., 2021). One of the most important threats for freshwater mussels in these regions is climate change and its effects on river hydrology (Benson et al., 2021). Mass mortalities of freshwater mussels from river drying and high temperature events are well documented across several Mediterranean regions (Sousa et al., 2018; Sheldon et al., 2020; Lymbery et al., 2021; Nogueira et al., 2021). The frequency and intensity of these events are expected to worsen under projected climate change scenarios with many perennial rivers becoming intermittent, and intermittent rivers experiencing longer and more severe periods of drying (Döll & Schmied, 2012; Cooper et al., 2013; Gomes-dos-Santos et al., 2019). It is therefore critical that desiccation and upper thermal tolerances of freshwater mussels in these regions are understood to inform their conservation and management.

One such region is Australia's Murray–Darling Basin, which covers a geographic range > 1 million km^2 and provides freshwater to ~ 2 million people (Leblanc et al., 2012) as well as almost 50% of the country's water for irrigation purposes (ABS, 2021). Water extraction and river regulation has resulted in major changes to natural flow regimes and reductions in stream flows in comparison to pre-European settlement levels (CSIRO, 2008). Hydrology in this region is further complicated by temperature and rainfall variability attributed to climate change (Hope et al., 2017; MDBA, 2019). Projected climate trends suggest an increase in temperature and overall yearly reduction in rainfall to occur in the southern basin where flow regimes are already a reflection of water demands rather than natural patterns (MDBA, 2019). Whilst historical records suggest intermittent drought and flooding are common across the northern Murray–Darling Basin, climate projections depict drought becoming more frequent and intense (Phelps & Kelly, 2019). During the most recent drought (2017–19) much of this region had record low rainfall (Aitkenhead et al., 2021) with several catchments exposed to prolonged periods (up to 458 days) of low or no flow (Sheldon et al., 2020).

Freshwater mussel species may vary widely in their physiological tolerance of emersion and their behavioural responses to habitat drying, with those that use their muscular foot to burrow within the sediment often being more tolerant of desiccation than those that horizontally track receding water (Gough et al., 2012; Mitchell et al., 2018). Once emersed, freshwater mussels can no longer feed and are required to persist in a state of aestivation. Freshwater mussels can regulate their gaping behaviour to survive long periods of time out of water, however, this leads to trade-offs with other survival mechanisms including efficient metabolism and preventing the build-up of toxic by-products (Byrne & McMahon, 1994).

The two most common freshwater mussel species in the Murray–Darling Basin are the river mussel *Alathyria jacksoni* Iredale, 1934 and the floodplain mussel *Velesunio ambiguus* (Philippi, 1847), both from the family Hyriidae. *Alathyria jacksoni* is endemic to the Murray–Darling Basin whereas the distribution of *V. ambiguus* further extends across Eastern Australia (Walker, 1981). *Alathyria jacksoni* is found in the main channel of large rivers and is not found in lentic environments (Walker, 1981). In contrast, *V. ambiguus* typically occurs in lakes, billabongs, impoundments, and small streams (Walker, 1981). Sheldon & Walker (1989) reported cohabitation of the two species along the Murray River, but with *A. jacksoni* in the deeper waters of the main channel and *V. ambiguus* restricted to sheltered pockets along the river margins. Neither *V. ambiguus* or *A. jacksoni* are currently listed as threatened by the IUCN Red List (IUCN, 2021) (although *A. jacksoni* is listed as data deficient), but evidence suggests extreme drought conditions over summer has resulted in both species undergoing mass mortality events (Mallen-Cooper & Zampatti, 2020; Sheldon et al., 2020). During the summer periods of 2017–2019, more than 2.9 million freshwater mussels were estimated to have perished, with 100% mortality estimated at some river sites (Sheldon et al., 2020). Walker (1981) reported that *A. jacksoni* was more susceptible to desiccation than *V. ambiguus*; at 18°C, 50% of *A. jacksoni* and *V. ambiguus* died in 12 and 280 days, respectively.

In the present study, we assessed the desiccation tolerance of *A. jacksoni* and *V. ambiguus* by simulating cease to flow events during drought conditions (i.e., increasing temperature and a drying substrate). The specific aim of the study was to compare the tolerance of *A. jacksoni* and *V. ambiguus* to desiccation in sediment at a range of upper thermal extremes. We hypothesized that *V. ambiguus*, because of differences in preferred habitat, would have a greater tolerance to desiccation than *A. jacksoni*, and that the desiccation tolerance of both species would decline with increasing sediment temperature.

Methods

Study species

Adult *A. jacksoni* were collected from the Mulwala canal (35.7771° S, 145.7552° E) in May 2021 and adult *V. ambiguus* from Mulwala canal (35.3866° S, 144.2489° E) in September 2020. Species were identified morphologically using keys within the Australian Freshwater Molluscs interactive resource (Ponder et al., 2020), and further confirmed via Sanger sequence analysis using the protocols outlined in Folmer et al. (1994). Mussels were transported to Narrandera Fisheries Centre (NFC; 34.78° S, 146.57° E), NSW Australia, located next to the Murrumbidgee River, where they were initially treated with 15 g l^{-1} salt solution for 15 min in accordance with animal quarantine procedures. To our knowledge, there are no reported studies on salinity tolerances of the freshwater mussel species studied, however these short duration exposures to elevated salinity were not expected to impact adult mussel survival. Mussels were then held for $\geq$ 2 weeks in 3000 l holding tanks and provided aeration and constant flow using river water where temperatures fluctuated seasonally.

Species identification was confirmed from tissue samples of 10 randomly selected individuals of each species. Samples sent to the Australian Genome Research Facility underwent nucleic acid extraction and sequencing using polymerase chain reaction (PCR). Sequences for a 710-bp region of the Cytochrome C Oxidase Subunit 1 (COI) gene were returned using the primers LCO1490 (5′ GGTCAA CAAATCATAAAGATATTGG 3′) and HCO2198 (5′ TAAACTTCAGGGTGACCAAAAAATCA 3′) (Vrijenhoek, 1994). These sequences were trimmed for quality using Geneious Prime software (2021.1) with a confidence interval of 0.1. Quality sequences were then run on the National Centre for Biotechnology Information's (NCBI) nucleotide Basic Local Alignment Search Tool (BLAST). Genetic assignment was consistent with morphological identification of *A. jacksoni* and *V. ambiguus*.

Sediment temperature field trial

To inform maximum sediment temperatures in the freshwater mussel desiccation trial, we assessed upper summer sediment temperatures across a range of conditions in a field trial. The trial was run over 12 days in January 2021 within the grounds of NFC. Two plots distanced 6 m apart were set up in an open and flat area. One plot was in full sun and the other was shaded with 70% UV light blocking shade cloth (Coolaroo, Braeside, VIC) representing extremes in natural levels of light along MDB rivers. Within each plot enough soil was removed to install four plastic trays (163 × 413 × 652 mm) so that tray tops were level with the surrounding soil. This ensured the surrounding soil buffered sediment temperatures, simulating natural conditions. The trays within plots were filled with either clay or sand sediment types in an alternating fashion. Sediment was sourced from the Murrumbidgee River, with clay and sand considered to be extremes in sediment type in MDB rivers. Within each plot, half of the trays were irrigated for 10 min daily using an automatic digital tap timer (Holman Industries, Osborne Park, WA). Treatments were applied in a way that every combination of sediment type, moisture type, and light type was administered. The field trial setup described allowed greater control over these variables compared to on a river bank.

In each tray, sediment temperature was measured by 6 pendant waterproof temperature loggers (MX2201, HOBO, Onset Computer Corporation, Bourne MA, USA): 3 in an exposed position on the sediment surface and 3 at buried subsurface position (the top of the logger being 2.5 cm deep) similar to Gough et al. (2012). A total of 48 temperature loggers were used, each recording at an hourly interval. We also retrieved hourly air temperature recordings over the trial period from the nearby NSW Department of Primary Industries weather station at Leeton, 25 km from NFC.

Daily mean air temperature ranged from 18 to 32°C throughout the trial (Fig. 1). Sun-exposed surface sediment conditions on dry sand or clay had daily mean temperatures ranging from 24 to 38°C. While sub-surface sediment conditions in shaded wet sand or clay had daily mean temperatures ranging between 15 and 23°C. Light levels, moisture levels and position (on or buried within the sediment) affected temperatures more than sediment type. The highest daily mean temperature recorded at the surface of sun-exposed dry sediment was slightly above 38°C, which informed the upper constant sediment temperatures used in the laboratory (41°C). This was under the assumption that a day-long exposure to fluctuating sediment temperatures in the field was equivalent to a day-long exposure to constant temperatures in the laboratory.

Freshwater mussel desiccation tolerance trial

Aquarium based experimental trials were used to assess lethal temperatures for 50% mortality of mussels (LT50) and lethal times required for 50% of mussels to reach mortality (T_{50}). LT50s were only assessed over a 10-day period because progressively lower temperature treatments would have been needed to accurately explore LT50s over longer periods. Specimens of *A. jacksoni* ($n = 105$) and *V.*

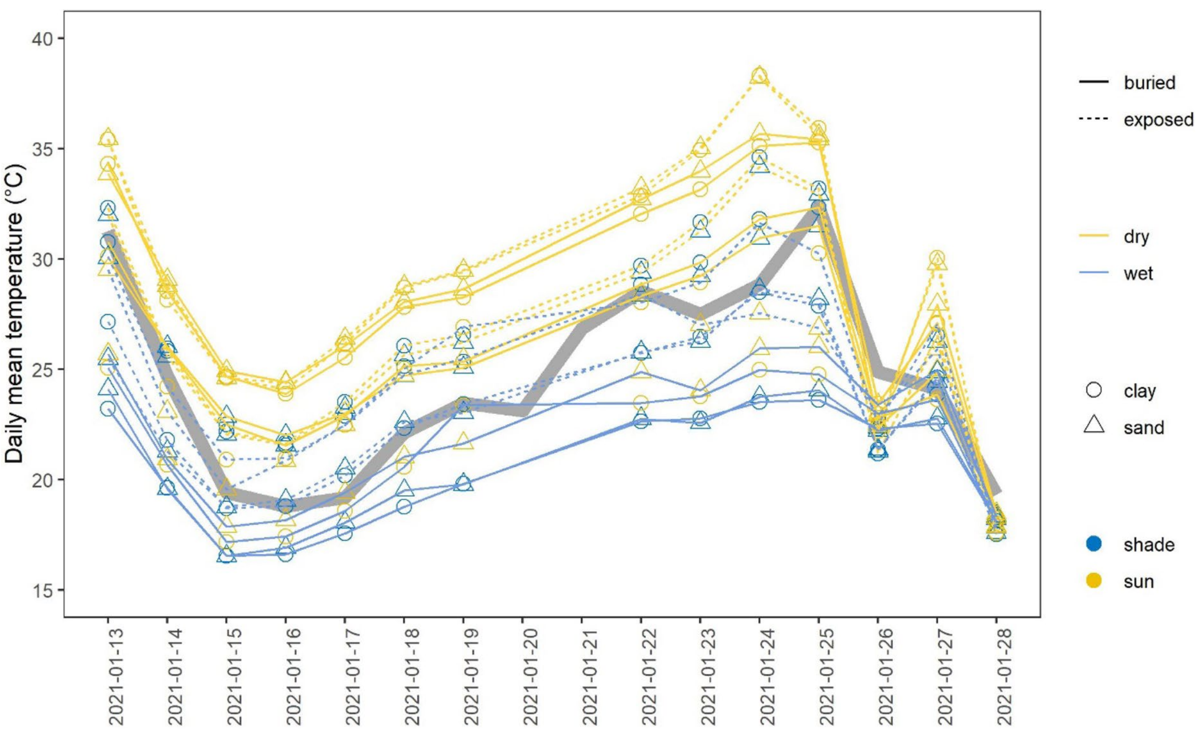

Fig. 1 Daily mean temperatures recorded by loggers in a range of sediment conditions (combinations of buried or exposed, dry or wet, clay or sand, and shade or sun) during the sediment temperature trial from 13 to 28 January 2021. The thick grey line indicates daily mean air temperature at the NSW DPI Leeton weather station. Sediment logger recordings on 20–21 January are not shown due to equipment malfunction

ambiguus ($n = 105$) were moved from holding tanks into 70 l experimental tanks filled with 40 l of recirculating bore water at a flow rate of 4 l min^{-1} with dissolved oxygen > 8 mg l^{-1}. Mussels from each species were acclimated to either a control temperature of 20 ± 1°C ($n = 30$) or a pre-experimental temperature of 26°C ($n = 75$). This temperature change was performed over a 5-day period at a rate of < 3°C per day, at which point temperatures were held for a further 4 days. Mussels were fed Shellfish diet 1800 (ProAqua Pty Ltd, Queensland) at ~ 3% of mean shell-free dry weight every 2 days.

After acclimation, mussels were added to one of three tanks within each of seven treatment groups: an in-water and a desiccation control, both at 20°C; and five desiccation treatments, at temperatures ranging from 29 to 41°C (Fig. 2). The trial design was adapted from Khan et al. (2020). This equated to five mussels of each species per tank and 15 mussels of each species per treatment group. Mussels allocated to the in-water controls were returned to conditions outlined in the acclimation period. Mussels allocated to desiccation controls and treatments were placed individually in 1 l plastic containers filled with fully saturated washed river sand. Containers with mussels were filled with sand to the 800 ml mark and mussels were buried so the top of the mussel was in line with the sediment surface. Containers were placed on

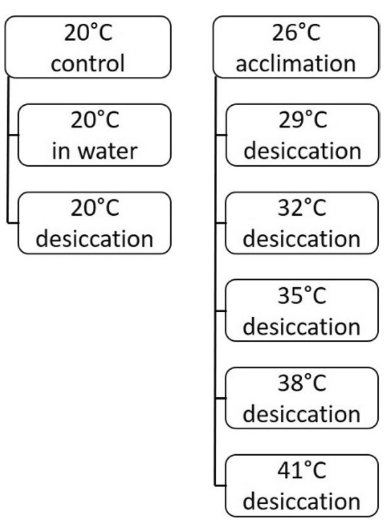

Fig. 2 Schematic diagram of experimental design showing acclimation and treatment conditions for in the freshwater mussel desiccation trial

aluminium stands in 70 l experimental tanks filled with 40 l of bore water providing a water bath and ensuring no water could enter the containers. The water in each tank was heated to the treatment temperatures using a 300-W titanium heater (Schego) connected to temperature controller unit (DC Series, Aqua Logic) (Fresh by Design, New South Wales). This experimental setup meant that each tank temperature was controlled independently and that a tank was a true replicate. Experimental desiccation conditions were similar to those described in Gough et al. (2012) with sediment moisture content declining over time; simulating river drying.

Sediment temperatures were measured hourly in each tank throughout the experiment using pendant waterproof temperature loggers (MX2201, HOBO) buried in an additional container filled with saturated washed river sand at the start of the experiment (5 cm deep). To document how sediment moisture content changed during the trial, this was measured in each tank within a second additional container filled with saturated washed sediment. A sediment subsample was weighed and incubated at 65°C for 3 days. The sample was then reweighed, and the resultant weight loss was used to determine the sediment moisture content using the equation:

$$\text{Sediment moisture content} = \frac{\text{Wet sediment weight(g)} - \text{Dry sediment weight(g)}}{\text{Dry sediment weight(g)}} \times 100$$

This was performed at day 0 (as mussels were added to tanks), 1, 4, 10, 20 and 40. Mussel survival was observed daily until day 20 and then every second day until day 73, when both species had reached 50% mortality. In-water and desiccation controls were monitored during the 10-day period informing lethal temperatures values, similar to Khan et al. (2020). Mortality was deemed to have occurred if a mussel was gaping and did not respond to gentle probing.

Data analysis

The LT50 and T_{50} values, and their 95% confidence intervals, were determined from survival information using two-parameter logistic regression curves, implemented in the drc package (Ritz et al., 2015) in R v2.12.0 (R Core Team, 2021). LT50 comparisons were also performed between species via the confidence interval ratio test (Wheeler et al., 2006) in the drc package. In this test, a ratio of LT50 estimates is compared with 1 and a 95% confident interval is determined around this ratio. If the confidence interval excludes 1, then the estimates are significantly different.

Results

Lethal temperatures (LT50)

Sediment temperatures throughout the experiment remained within 1.5°C of treatment temperatures. The only exception to this was a 22 h period on day 40–41 when sediment temperatures fell due to an electrical fault. Sediment moisture content was initially fully saturated with values > 5%. From that point, moisture levels decreased at a faster rate at higher temperatures (Fig. 3). The lowest sediment moisture level recorded was 0.01%. By day 20 all treatments were at or below 0.06%.

Mussels died sooner at higher temperatures in the simulated river drying conditions (Table 1). Over an acute 10-day exposure period of simulated river drying, LT50 estimates at a given time point did not differ between *A. jacksoni* and *V. ambiguus* mussels acclimated to 26°C. However, LT50 estimates were consistently higher in *V. ambiguus*. LT50 estimates for *A. jacksoni* fell progressively over time from 38.8°C at 1 day to 30.7°C at 10 days. In contrast, LT50 values for *V. ambiguus* fell steadily from 40°C at 1 day to 31.2°C at 10 days. For controls at 20°C either in water and fed throughout the experiment or under desiccation, no *V. ambiguus* mussels or *A. jacksoni* mussels died over this 10-day period.

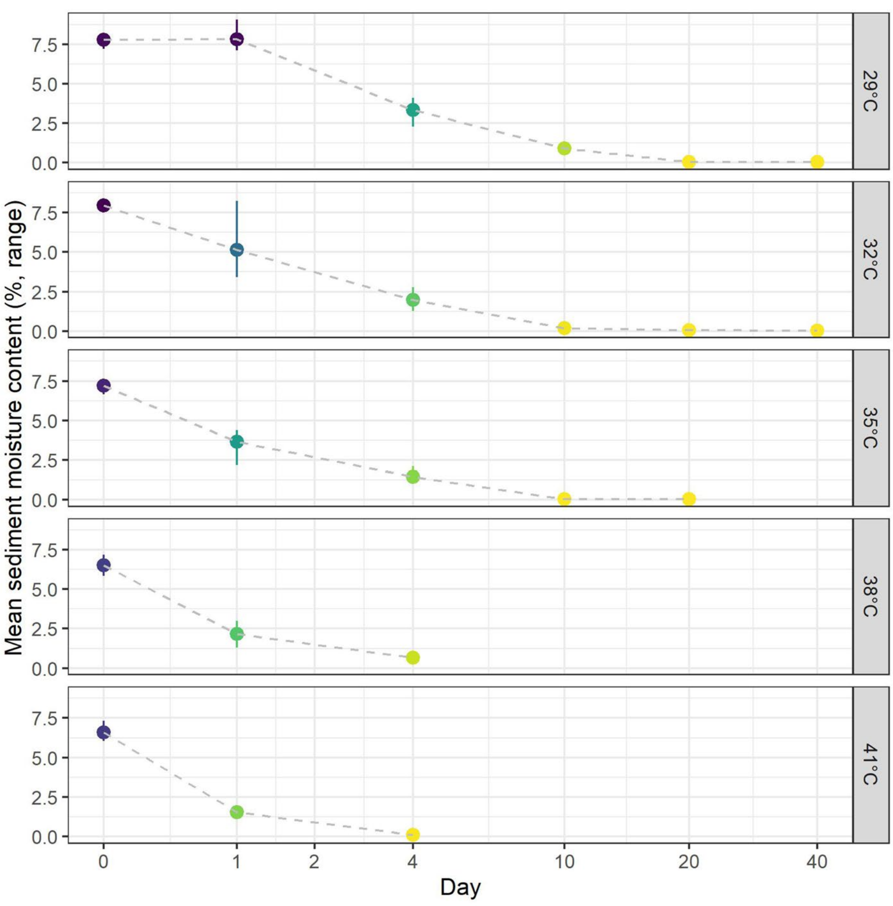

Fig. 3 Moisture content of sediment within containers holding mussels at 29, 32, 35, 38 and 41°C in the freshwater mussel desiccation trial. Points indicate mean values of measurements from individual tanks and bars represent ranges. Note that values are not shown once no mussels were alive for several days in a treatment

Table 1 LT50 values and 95% confidence intervals (CI) for *A. jacksoni* and *V. ambiguus* at 1, 2, 4 and 10 days in the freshwater mussel desiccation trial

Days	*A. jacksoni* LT50 (95% CI)	*V. ambiguus* LT50 (95% CI)	Confidence interval ratio test: estimate (95% CI)
1	38.8°C (38.0–39.6°C)	40.0°C (38.9–41.1°C)	0.97 (0.94–1.004)
2	34.7°C (33.9–35.5°C)	35.6°C (34.8–36.5°C)	0.97 (0.94–1.006)
4	32.8°C (32.1–33.4°C)	33.3°C (32.2–34.5°C)	0.98 (0.94–1.03)
10	30.7°C (29.5–31.8°C)	31.2°C (30.1–32.5°C)	0.98 (0.93–1.03)

Confidence interval ratio test results for comparisons of LT50 estimates between mussel species are also provided (estimates are significantly different when confidence interval excludes 1)

Lethal times (T_{50})

As for LT50, the T_{50} for both species also decreased at higher temperatures (Table 2, Fig. 4). These estimates were similar between species at higher temperatures (41°C: ~ 1 day, 38 C: ~ 1 day, 35°C: 2–3 days and 32°C: 10–13 days), although tended to be shorter for *A. jacksoni*. However, at 29°C, T_{50} estimates differed between *V. ambiguus* and *A. jacksoni*, with *V. ambiguus* surviving much longer than *A. jacksoni* (14 and 58 days, respectively) (Table 2).

Maximum survival times were 2 days at 41°C, 3 days at 38°C and 29 days at 35°C, while a subset of mussels were still alive at the end of the experiment for 29°C and 32°C treatments. While maximum survival times were similar between species at high temperatures of 41°C (2 days for both species) and 38°C (3 days for both species), differences became apparent at lower temperatures. For example, at 35°C, the maximum survival time of a *A. jacksoni* was 4 days, well short of *V. ambiguus* at 29 days.

Discussion

The present study found that *V. ambiguus* was more resistant to desiccation than *A. jacksoni*, as previously reported by Walker (1981). However, this increased resistance to desiccation was highly temperature dependent and was only apparent at the lowest emersion temperature tested.

A number of previous studies have examined the influence of temperature on tolerance of freshwater mussel species. Gough et al. (2012) and Mitchell et al. (2018) examined the survival of different mussel species after emersion at temperatures ranging between 25 and 45°C and found that survival times of all species were reduced at higher temperatures. Higher temperatures have a direct effect on mussel survival through cellular damage (Sørensen et al., 2013) and elevated metabolic rate that depletes energy stores (Golladay et al., 2004). Our desiccation experiment simulated a drying river, by starting with fully saturated sediments and then withholding water, allowing the sediments to dry over the course of the experiment. Sediment moisture content during

Table 2 T_{50} values and 95% confidence intervals (CI) for *A. jacksoni* and *V. ambiguus* at 29, 32, 35, 38 and 41°C in the freshwater mussel desiccation trial

Temperatures (°C)	*A. jacksoni* T_{50} (95% CI)	*V. ambiguus* T_{50} (95% CI)	Confidence interval ratio test: estimate (CI)
29	14.2 days (12.7–15.6 days)	57.8 days (39.4–76.2 days)	0.25 (0.16–0.32)
32	12.6 days (10.9–14.2 days)	10.3 days (7.4–13.06 days)	1.23 (0.85–1.59)
35	1.9 days (1.6–2.2 days)	3.4 days (2.4–4.3 days)	0.56 (0.37–0.74)
38	1.0 days (0.7–1.3 days)	1.3 days (1.0–1.5 days)	0.78 (0.49–1.06)
41	0.8 days (-1.7–3.4 days)	1.0 days (0.4–1.6 days)	0.82 (-1.86–3.50)

Confidence interval ratio test results for comparisons of T_{50} estimates between mussel species are also provided (estimates are significantly different when confidence interval excludes 1)

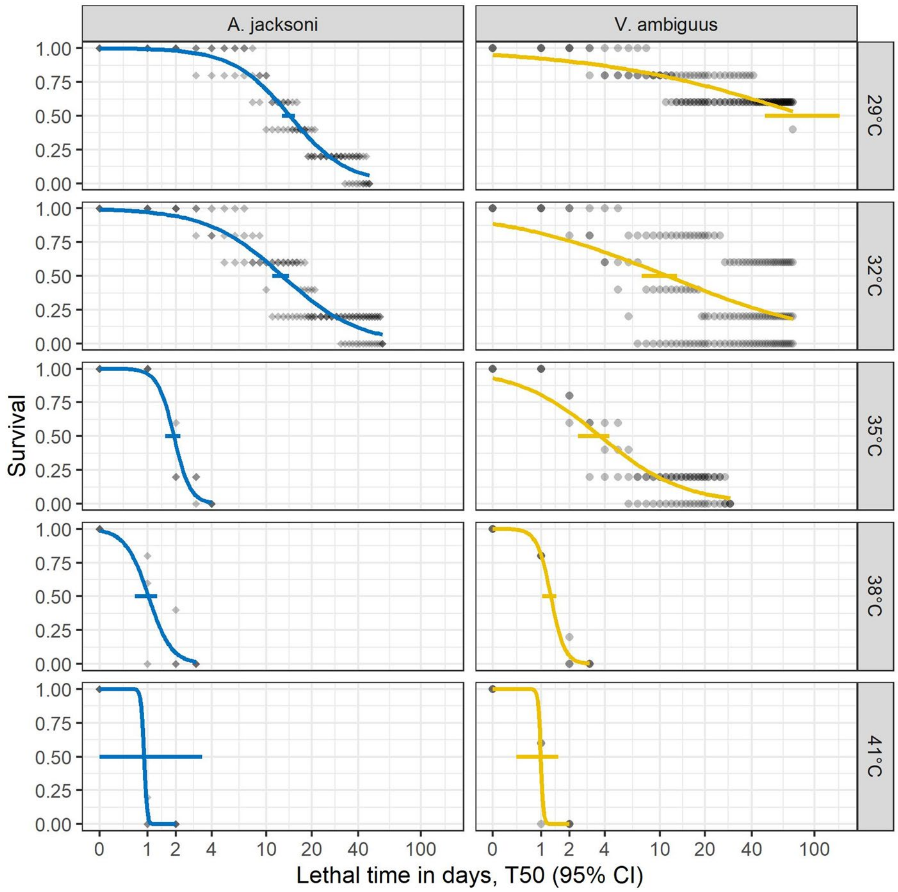

Fig. 4 Survival times of *A. jacksoni* and *V. ambiguus* mussels at 29, 32, 35, 38 and 41°C in the freshwater mussel desiccation trial. Points represent mussel survival at each assessment in a replicate tank, with point shading indicating the number of replicates with an identical survival value (darker colour for more replicates with the same value). Lines show the two-parameter logistic regression curves and are colour-coded by temperature. T_{50} values and 95% confidence intervals are also shown

the desiccation experiment decreased more rapidly at higher temperatures. Therefore, an increased rate of water loss from mussels in the higher temperature treatments likely contributed to shorter survival times (Lymbery et al., 2021).

While freshwater mussels are generally more tolerant of desiccation than both estuarine or marine bivalves (Byrne & McMahon, 1994) and other freshwater molluscs such as gastropods (Collas et al., 2014), there is still substantial variation among species (Gough et al., 2012; Newton et al., 2015; Mitchell et al., 2018; Nakano, 2018). This variation can often be related to differences in life history characteristics and habitat use. For example, Mitchell et al. (2018) studied the desiccation tolerance of five freshwater mussel species in Texas and found that the two species with lowest tolerance [(i.e., the Texas fatmucket *Lampsilis bracteata* (Gould, 1855) and the yellow sandshell *Lampsilis teres* (Rafinesque, 1820)] were found most often in deeper pools and lentic microhabitats that very rarely became completely dry. The greater physiological tolerance to desiccation of *V. ambiguus* is therefore likely to be an adaptation to more frequent drying associated with floodplain habitats.

The greater tolerance of desiccation by *V. ambiguus* compared to *A. jacksoni* is consistent with their documented tolerances to a range of other environmental stressors. Sheldon & Walker (1989) found *V. ambiguus* to be more tolerant than *A. jacksoni* to low oxygen levels. *A. jacksoni* is unable to regulate oxygen consumption when exposed to declining oxygen levels, whereas *V. ambiguus* can maintain a steady rate of oxygen consumption under hypoxic conditions and has a greater capacity than *A. jacksoni* to metabolise anaerobically (Sheldon & Walker, 1989). Under conditions of desiccation and severe oxygen stress, *V. ambiguus*, unlike *A. jacksoni*, is able to completely close its valves, forming an airtight seal and presumably relying on anaerobic metabolism

(Walker et al., 2001). *V. ambiguus* is also able to survive very high levels of blood ammonia, a two-fold increase in the ionic composition of body fluids and a weight loss of up to 40% (Ch'ng-Tan, 1968; Walker, 1981).

From a field-based perspective, our sediment temperature data also indicate that sediment temperatures at and near the surface can be greatly influenced by moisture content, exposure to the sun and position (surface or buried), but largely independent of sediment type (clay or sand). Temperatures were consistently lower within the sediment than on the surface and were further reduced by soil moisture and shade. Temperature loggers buried in moist, shaded sediment showed these conditions to reduce temperatures by $\leq$ 14°C in comparison to other treatments. A difference in temperature of this magnitude is likely to have a major impact on the ability of mussels to survive desiccation. Previous studies have found that desiccation tolerance of freshwater mussels is greatly enhanced by the presence of shade and the utilisation of moist microhabitats, for example by burrowing into sediment (Gagnon et al., 2004; Golladay et al., 2004; Lymbery et al., 2021). The mussel tolerance results from this study could help to define upper thermal thresholds and determine whether these thresholds are exceeded during river drying events (e.g. Khan et al., 2020). For example, mussels exposed to mean daily sediment temperatures of > 38°C (observed at the surface of sun-exposed dry sediment in the field trial) are likely harmful to both *A. jacksoni* and *V. ambiguus* (LT50 at 1 day: 38.8°C and 40.0°C, respectively; T_{50} at 38°C: 1.0 days and 1.3 days, respectively).

There are several other avenues of continued research to further understand the effects of desiccation and thermal extremes on freshwater mussels. The current study focused on adults collected from similar habitat types within the Murray–Darling Basin. Knowledge on the tolerance of freshwater mussels to desiccation and thermal extremes could be expanded across a range of demographics (i.e., comparisons between age groups, size classes, populations). Identifying behavioural responses to desiccating conditions at high temperatures could also provide further insights into species specific requirements during river drying events. This is especially important considering that we observed very large effects of subsoil depth, shade and soil moisture on sediment temperature. Regarding the current study species, Jones (2007) suggests *V. ambiguus* outperforms *A. jacksoni* in its ability to burrow into cooler sediment layers in response to emersion, although rapid water drawdown (Newton et al., 2015; Lymbery et al., 2021) and thermal stress could limit the extent of these behavioural responses (Archambault et al., 2014) even for proficient burrowers. This has potential implications for hydrological management, particularly in intermittent freshwater systems. Further research is required, however, to better understand the microhabitats used by these mussel species in drying rivers so that effective guidelines can be provided to river managers.

Our findings contribute to the growing evidence that increased temperatures and river drying under climate change will have detrimental impacts on the distribution and abundance of freshwater mussel species, particularly those in Mediterranean climates. Moreover, it highlights that species considered tolerant to desiccation may still be at risk when exposed to river drying at high temperatures. These risks should be considered by river managers and conservation practitioners in the context of the importance of freshwater mussels to aquatic ecosystem health. Avenues for protecting freshwater mussel populations during river drying include providing base flows to provide refuge for critical source populations, timing water delivery to minimise emersion of freshwater mussels during periods of extreme heat, and avoiding rapid water drawdowns at such times. Refugia could also be provided by maintaining and restoring riparian and floodplain vegetation to reduce surface and subsurface sediment temperatures. This would also benefit aquatic ecosystems more broadly, by increasing bank stability, and providing instream wood habitat and allochthonous carbon sources to support food webs (Medeiros & Arthington, 2011; Davis et al., 2015).

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Author contributions DWW, JDT, SJB, AJL, and SD contributed to conceptualisation. DWW and EB helped in developing methods, data analysis, and preparation of figures and tables. DWW, JDT, EB, SJB, AJL, SD conducting the research, data interpretation, and writing.

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

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Not applicable.

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