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Exploring the desiccation tolerance of the invasive bivalve *Corbicula fluminea* (Müller 1774) at different temperatures

Simone Guareschi ⬤ · **Paul J. Wood**

Abstract *Corbicula fluminea* (Müller, 1774) (Mollusca, Corbiculidae) is among the most successful and widespread invaders of aquatic ecosystems worldwide. Given its wide geographical distribution and documented effects on aquatic ecosystems, there is considerable interest in quantifying its behaviour, propagation and control. We conducted a series of laboratory experiments to assess the effects of complete desiccation (aerial exposure at high relative humidity) on a UK population of *C. fluminea* for: (1) different environmental temperatures (6 scenarios: from cool winter droughts to summer heatwave thermal conditions); and (2) two size classes (> 1 cm and ≤ 1 cm). A mortality rate of 100% was obtained for all experiments, except the lowest temperature scenario of 4 °C. For both high-temperature scenarios (25 and 30 °C) 100% mortality was recorded after 48 h, and an elevated mortality rate recorded after 24 h. An extended period of desiccation of 5–6 days would be necessary to reach a mortality rate of 90% at 15 °C and 3.5 days at 20 °C. Statistical analysis demonstrated a significant effect of temperature on mortality, but both size classes displayed similar responses to desiccation. The greatest difference in mortality was recorded between the highest and lowest experimental temperatures. *C. fluminea* was particularly tolerant to desiccation when low temperature and high humidity conditions coincided, suggesting it could potentially spread to regions beyond its current eco-geographical range. The results will be of direct interest for regulatory authorities considering desiccation (and water level management) as a means of managing and preventing the further spread of this species.

Keywords Biological invasions · Physiological trait · Alien species · Asian clams · Dewatering · Droughts

Introduction

Biological invasions represent some of the most important threats to biodiversity globally and understanding their effects, consequences and potential ways of managing them represent major challenges for pure and applied science (e.g., Simberloff et al. 2013; Havel et al. 2015; Bellard et al. 2016). Freshwater ecosystems have been heavily invaded (Strayer, 2010) and among invertebrate invaders, molluscs and

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crustaceans are the most frequently groups recorded (Karatayev et al. 2009; Fenoglio et al. 2016).

Corbicula fluminea (Müller, 1774) is a freshwater bivalve (Mollusca, Corbiculidae), commonly called "Asian Clam", originating from Southeast Asia (Gomes et al. 2016). It has a yellow–brown globular shell, usually < 30 mm width (Zieritz, 2016), and is both a filter- and pedal-feeder in benthic ecosystems (Hakenkamp et al. 2001). It is considered among the most widespread and hyper-successful invaders in aquatic ecosystems globally due to its highly effective traits including: rapid growth, high fecundity with both sexual and asexual reproduction strategies, high dispersal capacity and its strong association with human activities including aquaculture (Sousa et al. 2008a; Jou and Liao 2006; Ilarri et al. 2011; Verbrugge et al. 2012; Sousa et al. 2014; Laverty et al. 2015).

C. fluminea has been present in Europe (Portugal and France) since at least the early 1980s (Mouthon, 1981, see Sousa et al. 2008a for a complete invasion history). Its invaded geographic area appears to be expanding within regions it has already successfully colonised (e.g., Spain—Zamora-Marín et al. 2018), encompassing wide climatic conditions from semi-arid northern Africa (Morocco, Clavero et al. 2012) to northern Europe (North Russia—Bespalaya et al. 2018), with further expansions predicted due to climate change (Gama et al. 2017).

It is listed among the "worst invaders" within Europe (Nentwig et al. 2018), considered one of the five most important freshwater suspension feeding invaders (Karatayev et al. 2007) and has been identified as a high-risk aquatic invasive species in Great Britain (Gallardo and Aldridge 2013). The first record of *C. fluminea* in England was in 1998 (Baker et al. 1999) and it is currently recorded and abundant in several UK rivers (including the River Thames and numerous tributaries, Elliott and zu Ermgassen 2008). Moreover, the extensive navigation network of England allows inter-basin transfers of water, which may facilitate the expansion of its range (Gallardo and Aldridge 2018).

As a major freshwater bio-fouler (Nakano and Strayer 2014) it can form large agglomerations of live individuals and the dead shells may form extensive benthic deposits on riverbeds and in artificial waterbodies (e.g. drainage channel infrastructure). Biofouling and impairment of water-dependent industries in the USA (e.g., Johnson et al. 1986) and within irrigation systems in Europe have been reported (e.g. Rosa et al. 2011).

In both natural and regulated rivers, *Corbicula fluminea* typically becomes one of most important components of benthic fauna in terms of abundance and biomass once established (e.g. Sousa et al. 2008b). This can result in major changes to other faunal and floral populations including submerged macrophytes, phytoplankton, zooplankton and for biogeochemical cycling (see Sousa et al. 2008a for details). In addition, negative effects on indigenous freshwater bivalve populations have been recently reported on the Iberian Peninsula (Ferreira-Rodríguez et al. 2018) and UK (Lopes-Lima et al. 2017).

Due to its widespread distribution and high densities across many aquatic habitats, from lotic systems to lakes and estuarine zones (Rosa et al. 2011), there is considerable interest in the behaviour, propagation, economic impacts management and control of *C. fluminea* (Doherty and Cherry 1988; Ortmann and Grieshaber 2003; Sousa et al. 2009; Rosa et al. 2011; Crespo et al. 2015; Coughlan et al. 2019). Eradication of *C. fluminea* would appear unrealistic in most circumstances, whereas control activities may prove more promising (Sousa et al. 2014). Aquatic disinfectants, including bleach and salt solutions have been tested as control measures in aquaria, and laboratory methods developed exposing individuals directly to hot steam or contact with dry ice have recently been described (Coughlan et al. 2018, 2019). However, control measures for invasive aquatic organisms require maximum efficacy whilst minimising wider environmental and ecological damage (e.g. impacts on no-target organisms or downstream river sections) when applied in the field. Among abiotic variables, thermal tolerances appear to be a primary factor influencing the fitness and potential spread of *C. fluminea* populations (Weitere et al. 2009; Müller and Baur 2011). For instance, Werner and Rothhaupt (2008) reported that winter water temperatures < 2 °C for several weeks limited survival rates of *C. fluminea* in Lake Constance (Central Europe) while McDowell et al. (2014) indicated that the minimum air temperature may influence its distribution within the USA.

In the temperate zone, elevated water and air temperature, and river channel drying (desiccation) is typically associated with summer drought and

heatwaves, although flow cessation and channel drying may occur throughout the year (e.g. Folland et al. 2015; Tolonen et al. 2019). Desiccation resistance has been shown to affect the distribution of many aquatic invertebrate taxa (e.g. Ricciardi et al. 1995; Pallarés et al. 2016). Given predicted climate change and drought intensification scenarios (Prud-homme et al. 2014) a greater understanding of the response and adaptably of aquatic invaders like *C. fluminea* may aid in forecasting how its distribution may change or help target control measures. For molluscs, the effect of bivalve size on stress tolerance and mortality rates has been reported to be highly variable and potentially influenced by thermal regimes. Smaller clams have been hypothesised to be more susceptible to thermal shock than larger individuals in some settings (Werner and Rothhaupt 2008; Coughlan et al. 2018) while Byrne et al. (1988) reported increased size had a negative effect on mortality at temperatures of 25 °C and 35 °C. As a result, there is an urgent need to improve our knowledge regarding desiccation tolerance and drought resistance of *C. fluminea* to inform the development of biosecurity tools for controlling and preventing its further spread; especially in temperate regions where populations are expanding rapidly (Elliott and zu Ermgassen 2008).

To address this research gap and provide thermal and desiccation tolerance information, we conducted a series of laboratory experiments to assess the effects of desiccation (aerial exposure) on a UK population of *C. fluminea* for: (1) different environmental temperatures (4, 11, 15, 20, 25, 30 °C) and (2) two size classes. Experimentally testing the effects of exposure to different air temperature regimes will provide a better understanding of the desiccation tolerance of *C. fluminea* under varying climatic conditions (e.g. winter drought through to summer heatwave thermal conditions). Examination of different size classes will allow better characterization of which acts as the most effective propagule in response to drought/desiccation conditions. We hypothesized that increasing air temperature reduces *C. fluminea* survivorship, and that mortality rates are influenced by body size.

Methods

Study area and field work

Specimens of *C. fluminea* (Bivalvia, Corbiculidae) were collected from Hermitage Brook (WGS84 52°46′02″N; 01°11′27″W, altitude: 41 m a.s.l.) a 2.5 km watercourse that links the Grand Union Canal Leicester Navigation with the River Soar (Leicester-shire, UK). The waterway supported an abundant population of *C. fluminea* and can be considered a representative section of the large waterway network that links anthropogenic and natural waterbodies in lowland England.

Sampling was undertaken during late spring—early summer 2019 (May- early July) when flow was close to baseflow conditions and as a result, physico-chemical variables were relatively stable over the study period: temperature 17.5 ± 1.8 °C (mean $\pm$ SD), conductivity 616 ± 89 μS/cm and pH 7.6 ± 0.06.

Based on the maximum shell length, *C. fluminea* individuals were separated in two size classes in the field using a sieve: (1) "adults" (> 1 cm) and (2) "juveniles" (≤ 1 cm). Size is typically a good proxy of age and development stage in bivalves; for instance, Caffrey et al. (2011) referred to the one-year old cohort when shell height was less that 11 mm and Sousa et al. (2008a) classified *C. fluminea* individuals of 10 mm or greater as adults.

Laboratory experiments

Specimens were kept in the laboratory for 24 h (20 ± 1 °C) in aerated tanks containing water from the collection site to confirm survivorship and normal feeding behaviour before starting each experiment. Pilot experiments were conducted to test the experimental procedure in order to avoid confounding effects due to starvation (maximum length of each treatment was set to 10 days). Each experiment was conducted at a constant temperature in an environmental chamber (TAS, Series 3, England) with relative humidity (RH) maintained at around 80% ($81 \pm 4\%$, mean $\pm$ SD). The constant high RH in all the desiccation treatments allowed us to focus on the effects of temperature and size of individuals. A total of six temperature scenarios were tested for each size class (4, 11, 15, 20, 25, 30 °C). The coldest scenario

represents a winter drought scenario, typical of average air temperatures during January in the UK (period 1981–2010, https://www.metoffice.gov.uk/climate/uk/summaries/actualmonthly). The higher temperature scenarios (25 and 30 °C) were both higher than the mean daily maximum temperature during summer (July and August) for the period 1981–2010 and were used as analogies for periods of sustained high temperature under potential future climate change conditions. The remaining thermal treatments (11, 15, 20 °C) reflect conditions typical of spring to summer in the UK.

Following the acclimation period, for each temperature scenario, 100 individuals of each size class were dried on blotting paper and placed individually into clean 50 mL open plastic thermal resistant vials so that individual *C. fluminea* were not in contact with each other. A further 20 individuals per size-class were placed in a 15 L aquarium at the same experimental air temperature and used as a control not subjected to desiccation stress. Overall, the experiments included 1200 individuals (100 individuals *6 scenarios * 2 sizes = 1200 ind.) and 240 individuals were used for controls. For each scenario, every 24 h, ten individuals were selected at random from each size-class (adults and juveniles) and immersed in water to determine the number of individuals alive (see SM1 for a scheme). Mortality was deemed to have occurred if individuals did not commence filtering or move within 2 h. In addition, mortality was considered to have occurred if shells were found open before immersion in water. For shells that were closed, mortality was confirmed if: i) there was a pool of fluid around the shell (due to the emptying of the mantle cavity water store) or ii) the smell of decomposing body tissue.

Statistical analysis

To assess the effect of "size" (adults and juveniles), "temperature" and their interaction, linear modelling (*aov* function in Stats package) was undertaken using mortality rate as the dependant variable. Potential differences in mortality rates among temperature scenarios were tested by applying the post hoc Dunn test (Dunn 1964) appropriate for comparing unequal sample sizes (Zar 2010). This test performs multiple comparisons following a Kruskal–Wallis test providing both z-test-statistics and the *p* value for each pairwise comparison. Model residuals were

graphically checked for normality (confirmed by Shapiro–Wilk test, after logit transformation: log ($Y/[1 − Y]$)) and homoscedasticity assumptions (Zuur et al. 2009).

In addition, two different thermal tolerance indicators were calculated: lethal temperature (LT) and lethal time (lt) for two different mortality scenarios (50% and 90%) using a generalised linear model procedure (GLM: Crawley 1993). For these models the response variable only had two states (alive or dead) and a binomial distribution (quasibinomial when overdispersion was detected) was applied using the function *dose.p* in the MASS package (Venables and Ripley, 2002). The LT50 (defined as lethal temperature to reach 50% mortality at a specific time) and LT90 were tested for three fixed time scenarios (after 2, 5 and 7 days) and for both size classes to obtain a detailed comparison of trends.

Lethal times (lt50 and lt90) were calculated using the GLM approach outlined above but using time ("day") as an independent variable. The lt50 and lt90 represent the time (number of days) required to reach a mortality rate of 50% and 90% respectively and were calculated for each temperature scenarios. All statistical analyses and graphical presentations were undertaken within R v. 3.6.2 (R Core Team 2018).

Results

Temperature and size class

For all scenarios tested (6 temperatures and 2 size classes), a mortality rate of 100% was obtained except for 4 °C (50% and 80% mortality for adults and juveniles respectively). The quickest response in mortality was obtained for the high-temperature scenarios (25 and 30 °C, Fig. 1-2) with 100% mortality recorded after 48 h and elevated mortality rates recorded after 24 h (minimum values of 40–50% at 25 °C). In contrast, survivorship observed for the control groups kept in water at the same temperature averaged 90% at the end of each temperature treatment (min = 70%; max = 100%), with lowest survivorship (70–80%) recorded at the end of the 30 °C air-temperature control treatment.

Analysis demonstrated a significant effect of air temperature ($F_{(1,62)}$ = 19.42, $p < 0.001$), but no difference in mortality rates between the two size classes
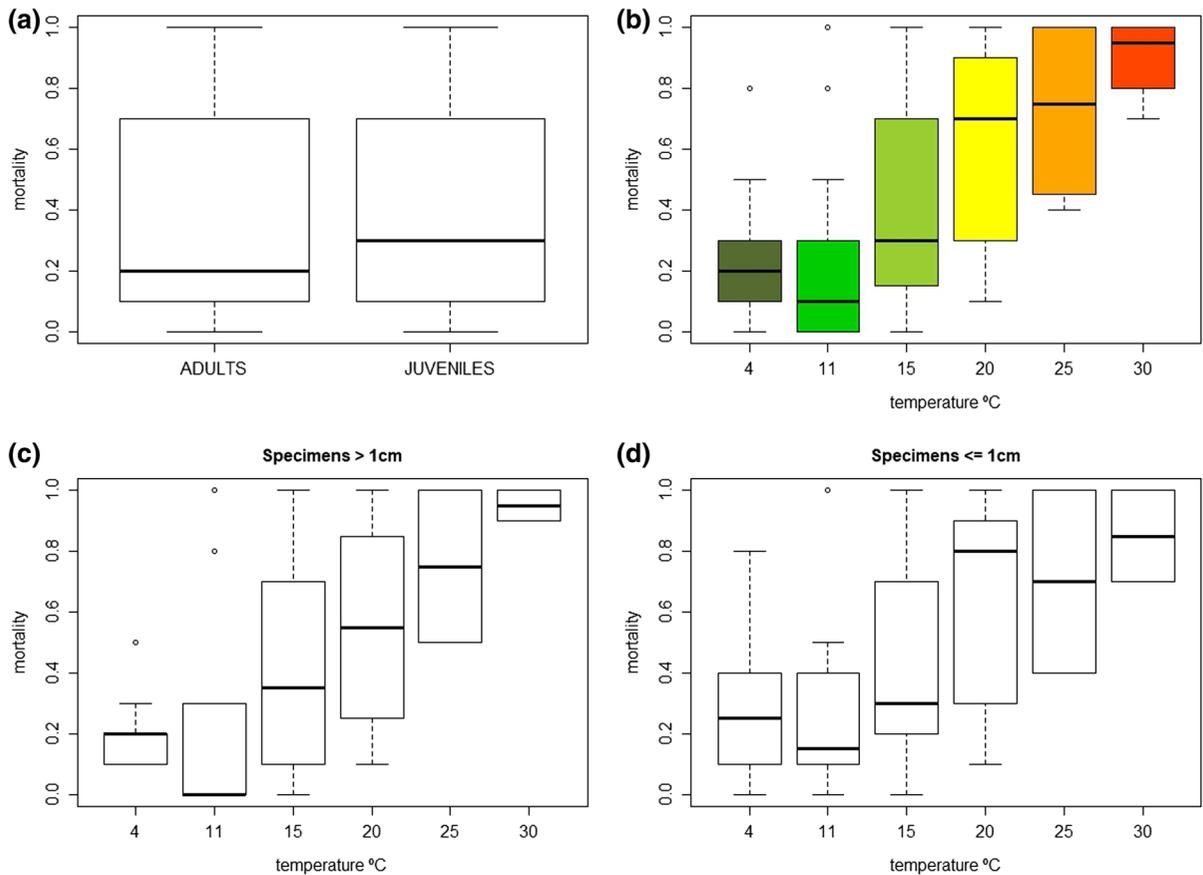
Fig. 1 Boxplots of *Corbicula fluminea* desiccation responses (percentage mortality) at different temperatures and size-classes. **a** comparison between adults and juvenile responses, **b** response for different temperature scenarios (see colour in Fig. 3); **c** Adult response for different temperature scenarios; **d** Juvenile response for different temperature scenarios. The median is denoted by the bold horizontal line, the box delimits the interquartile range, and the whisker lines extend to the observed maxima and minima

was observed ($p > 0.05$ and see Figs. 1, 2 and 3). In addition, the interaction between size classes and temperature (size class: temperature) was not statistically significant ($p > 0.05$).

Given that size class was not significantly different, pairwise analysis among temperature treatments were examined using the whole dataset (n = 66). Dunn's test indicated the largest differences in mortality were obtained for the extreme high (25–30 °C) and low (4–11 °C) temperature scenarios (Table 1).

Lethal temperature and lethal time values

The response of *C. fluminea* during desiccation experiments for the three different time steps considered (day 2–5–7) and for both size classes are shown in Fig. 3. The lethal temperature (LT50 and LT90) and lethal time (lt50 and lt90) values are presented in Table 2 and Table 3 respectively. Lethal temperatures (LT, Table 2) decreased over time in all instances (from day 2 to day 7) and the responses were comparable for both size classes (see also Fig. 1 and Fig. 3).

The LT50 was reached after two days at a temperature just below 20 °C (19.1–19.2 °C), while the LT90 was around 27 °C, but in both instances displaying the largest standard errors. After 5 days LT values decreased to 13 °C and between 16 and 18 °C for LT50 and LT90 respectively for both size classes. The results were more heterogeneous after 7 days of desiccation exposure with temperatures that ranged
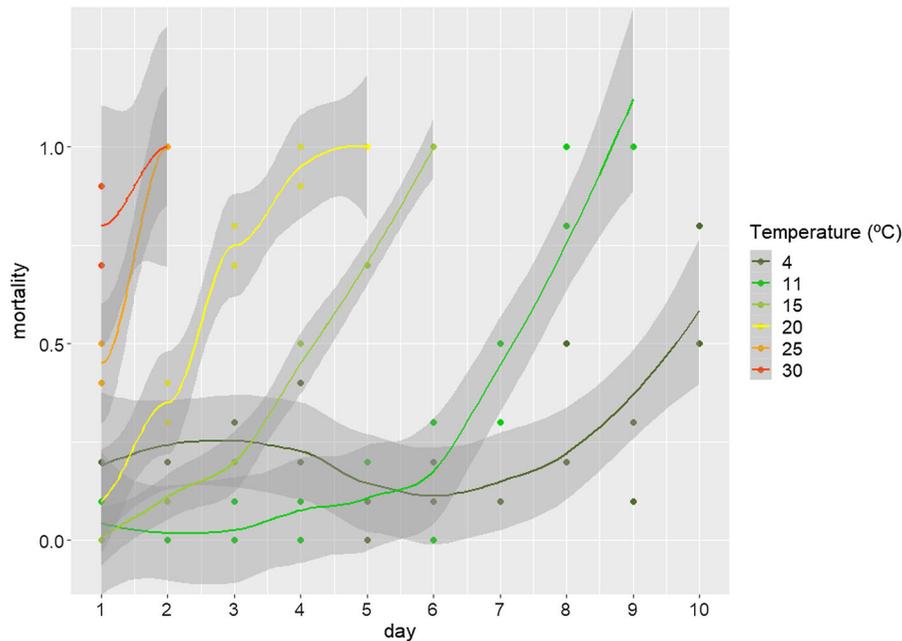
Fig. 2 *Corbicula fluminea* desiccation responses (percentage mortality on y-axis) for different temperature scenarios from day 1 to day 10. Loess curves with standard errors (dark grey) are displayed. Light grey space outside the range 0–1 on the y-axis is displayed to allow interpretation. Reduced number of points at 15 °C is due to overlapping

between 9 °C and 11 °C for LT50 and 14–15 °C for LT90 (see Table 2).

Lethal time results largely confirmed the LT outputs for each temperature scenario tested (Table 3) and demonstrated that at 25 °C and 30 °C the lt50 and lt90 was reached after 1 day (24 h), while periods of about 1 week (7 and 8.5 days) were required at 11 °C for lt50 and lt90 respectively. Intermediate values were obtained for 15 °C and 20 °C treatments. At 4 °C lethal times increased to around 10 days for lt50 (see Table 3 for details).

Discussion

The present study provides new knowledge regarding the desiccation resistance of the highly successful invasive species *C. fluminea*. As far as we know, this represents the first experiments addressing desiccation tolerances of *C. fluminea* over a wide range of temperatures (simulations from winter through to summer drought and future climate change conditions) for a UK population. The potential desiccation tolerance of the species was noted by Baker et al. (1999) when first recorded in the UK (Norfolk) as a

single *Corbicula* specimen was found to be alive ten days after collection within the sample net, although no further abiotic information was provided regarding the conditions it was found in.

We found evidence to support our first hypothesis, that different temperatures had a significant effect on mortality rates. The greatest differences were recorded between the lowest and highest temperature scenarios: at 30 °C 100% mortality was recorded after two days (48 h) while at 4 °C some specimens survived until the end of the experimental period (ten days).

Non-native bivalves from the genus *Dreissena* (*D. polymorpha* and *D. bugensis*) introduced in Canada survived emersion for up to 10 days at 10 °C (95% relative air humidity) and the authors suggested that individuals may also survive transport overland (Ricciardi et al. 1995). Similarly, our results for *C. fluminea* at 11 °C indicated survivorship after 1 week of desiccation (lt50 = 7.3 days). Lower temperatures (e.g., 4 and 11 °C with high relative humidity around 80%) appear to favour desiccation tolerance of invasive bivalves like *C. fluminea*. These findings highlight the importance of considering different air-temperature scenarios on the survival capacity of organisms subject to drought and desiccation stresses.
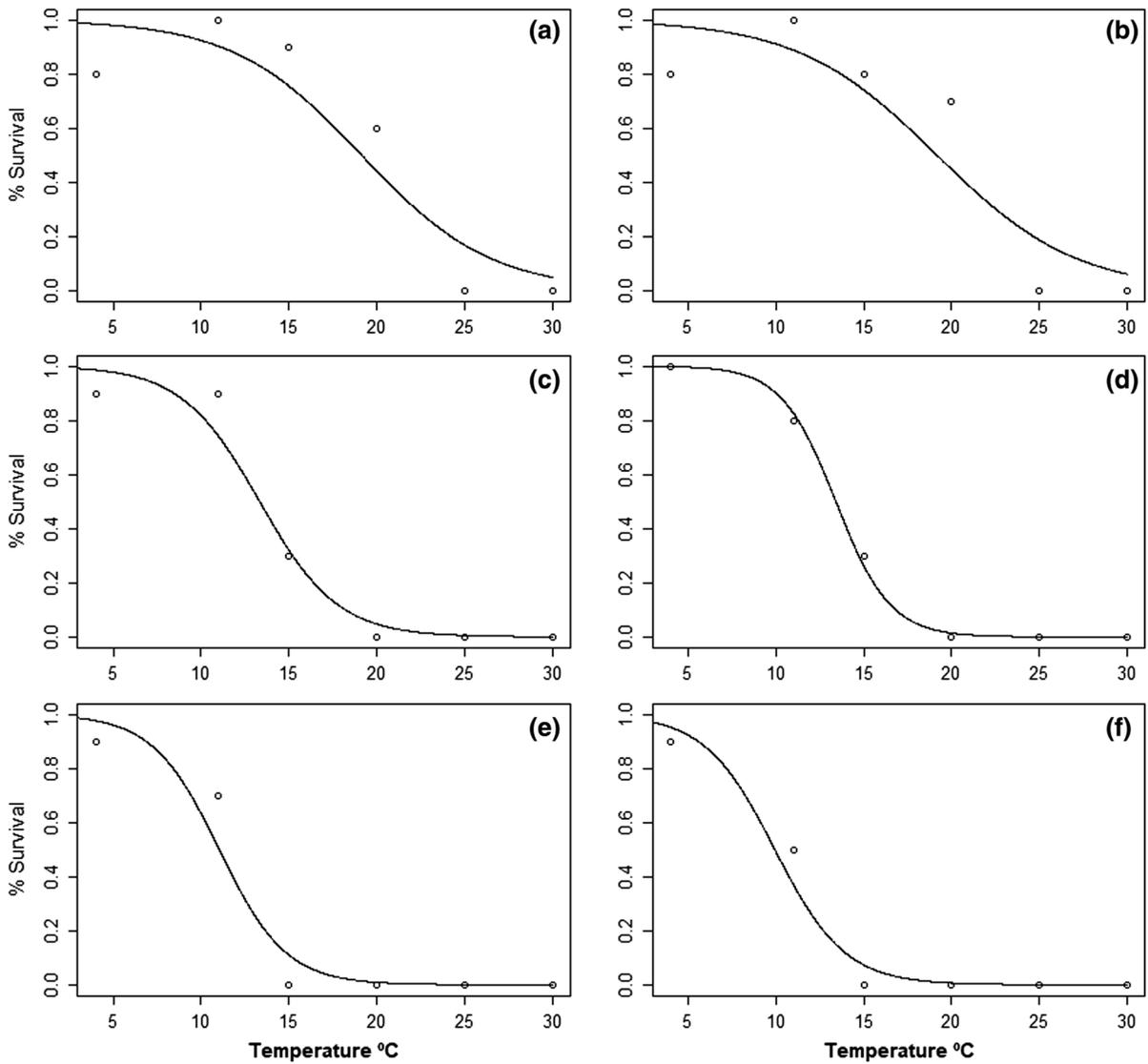
Fig. 3 Response of *C. fluminea* to desiccation at different temperature scenarios (percentage survival on the y-axis) for three different time period: day 2 (**a**, **b**), day 5 (**c**, **d**) and day 7 (**e**, **f**). Adult responses are displayed in the left column (letters **a**, **c**, **f**). Adult responses are displayed in the left column (letters **a**, **c**, **e**) while juveniles are displayed on the right (**b**, **d**, **f**). Data were fitted (survival curves) to a binomial GLM from which LT values were obtained

Table 1 Dunn test pairwise comparison of mortality values for different temperature scenarios. *Z* test-statistics are provided

Temp °C	4	11	15	20	25	30
4		− 0.62	0.93	1.97*	2.31*	2.78**
11			− 1.44	− 2.41*	− 2.64**	− 3.11**
15				− 1.03	− 1.60	− 2.05*
20					− 0.79	− 1.22
25						− 0.36

*p < 0.05: **p < 0.01

Table 2 Lethal Temperature (LT) for the 50% (LT50) and 90% (LT90) for *C. fluminea* size-classes and duration times (2–5–7 days)

Tolerance indicator	Dose	SE	Time (day)	Size
LT50	19.14	3.58	2	Adults
LT90	27.20	6.35	2	Adults
LT50	19.16	3.37	2	Juveniles
LT90	27.87	6.14	2	Juveniles
LT50	13.33	1.02	5	Adults
LT90	18.22	1.68	5	Adults
LT50	13.40	0.22	5	Juveniles
LT90	16.80	0.36	5	Juveniles
LT50	11.03	1.16	7	Adults
LT90	15.20	1.70	7	Adults
LT50	9.93	0.82	7	Juveniles
LT90	14.31	1.09	7	Juveniles

Dose (temperature in °C) and Standard error (SE) are provided

Table 3 Lethal time (lt50 and lt90) as number of days for *C. fluminea* during desiccation experiments

Tolerance indicator	Dose (no. days)	SE	Temp (°C)
lt50	0.90	–	30
lt90	1.00	0.05	30
lt50	1.00	0.03	25
lt90	1.09	–	25
lt50	2.29	0.16	20
lt90	3.52	0.28	20
lt50	4.02	0.18	15
lt90	5.63	0.31	15
lt50	7.31	0.23	11
lt90	8.47	0.36	11
lt50	10.44	3.08	4
lt90	21.70	9.57	4

Analysis have been run with adult size data except for the 4 °C scenario because adults' mortality was never > 50% along the treatment (max = 50%). Dose (number of days) and Standard error (SE) are provided. Symbol "–" = algorithm did not properly converge

Given the predicted increase in drought frequency and intensity in the UK (Rahiz and New 2013), these results have potential implications for the spread, management and control of invasive bivalves. The results highlight that the persistence and distribution models of invasive species within freshwater ecosystems should consider species desiccation tolerances. Even intermittent streams (systems with periodic drought and drying periods) rarely subject to invasion by aquatic taxa in most instances (Chiu et al. 2017) could experience limited invasion of *C. fluminea* if low temperatures and high humidity coincided (e.g. high latitude or high altitude site), although further field and laboratory research is required. The ability to rapidly disperse and establish populations in new geographic areas illustrates the success of this invasive species (e.g. Crespo et al. 2015). Our result suggests further expansions of the geographical range of *C. fluminea* is possible, covering a wider range of waterbodies and latitudes within its thermal tolerances. However, harsh winter conditions (spanning several weeks) may limit its survival and dispersal capacity (Werner and Rothhaupt 2008).

Median desiccation tolerance times for *C. fluminea* individuals from an outflow of Lake Benbrook (Texas, USA) at 35 °C (with a mean humidity of 75%) of 24 h were obtained by Byrne et al. (1988) and are comparable to this study (despite specimens being placed on a desiccator plate rather than in individual vials). Greater differences might be anticipated for 25 °C and 15 °C scenarios, with north American populations displaying lt50 values greater than those recorded in the present study (78 and 305 h compared to 24 h and 96 h). These differences probably reflect the natural climatology of the two areas: Texas (USA) classified as humid subtropical (Köppen–Geiger classification *Cfa*; Peel et al. 2007) while Leicestershire (England) is considered oceanic (*Cfb*) with greater differences between summer temperatures. Differences in the responses of *C. fluminea* inhabiting different climatological regions may reflect trait plasticity and the ability of individuals to survive desiccation stresses more effectively in subtropical climates. This may also reflect the longer time that *C. fluminea* has inhabited freshwater bodies in Southwest USA compared to the UK. The first USA records date back to the 1920s (Sousa et al. 2008a) and Texas was colonised and invaded during the 1960s (Howells, 1992); compared to the first records at the end of the 90 s in the UK. In addition, the presence of different invasive lineages in North America and Central Europe has been proposed (Gomes et al. 2016) and may account for differences in desiccation tolerances between populations.

Interestingly, Collas et al. (2014) examined the effects of desiccation on *C. fluminea* collected under similar climatological conditions (the Netherlands, Central Europe, *Cfb* climate) and reported a lt50 (lethal time) of around 200 h at a fixed temperature of 20 °C (with average RH of 68%). This is much longer than the 2.29 days (55 h) recorded in the current study and probably reflects some differences in experimental design, humidity values, acclimation periods and frequency in individual checks.

High humidity has been identified as a key factor influencing the behaviour, spread and drought tolerance of other molluscs (e.g. *Lottia gigantea* Miller et al. 2009), other invasive faunal species in desiccation tolerance experiments (*Procambarus virginalis* Guo et al. 2019) and the introduced marine alga, *Codium fragile* ssp. *tomentosoides* (Schaffelke and Deane 2005). Moreover, the importance of residual humidity between substrate interstitial pores has been recognised for some invasive mussels (e.g., Montalto and Ezcurra de Drago, 2003); but this may not be the case for *C. fluminea,* as it does not typically form clusters of individuals. Similarly, moist substrates significantly increased the survivorship of another hyper-successful aquatic invader (*D. polymorpha*) when exposed to the atmosphere (Paukstis et al. 1999). Our findings underline the need for caution when generalizing the effects or exposure/desiccation of species without comprehensive information regarding other abiotic factors (e.g., substrate composition and moisture) and specific geographic context. In addition, Crespo et al. (2015) also stressed the high ecophenotypic plasticity of *C. fluminea* and that it may not be possible to generalise some patterns or trends globally.

We did not find evidence to support our second hypothesis, that body size influenced the desiccation tolerance of *C. fluminea*. No significant differences in mortality were recorded between adults and juveniles, with both displaying similar median lethal temperatures and response (Table 2, Fig. 1 and 3). The absence of a specific effect of size on desiccation tolerance contrasts with some patterns reported for *C. fluminea* in other studies (see Byrne et al. 1988 in USA; Werner and Rothhaupt 2008 in Central Europe). Variable desiccation tolerances in relation to size have also been reported for *D. polymorpha*, with larger individuals being reported to be more resistant to aerial exposure than smaller individuals (Ricciardi

et al. 1995; Paukstis et al. 1999), while Tucker et al. (1997) indicated that smaller zebra mussels had an advantage in some situations (e.g. when individuals settled in substrate pore spaces). However, other invasive bivalves such as *Limnoperna fortunei* (Dunker, 1857) (Bivalvia, Mytilidae) displayed increased desiccation tolerance, with the size of individuals in laboratory trials (Montalto and Ezcurra de Drago 2003).

It should be noted that in the current desiccation experiments the individuals were unable to move vertically and had no opportunity to seek refuge (burrowing) within the substrate. However, field observations indicate that *C. fluminea* individuals typically live just beneath the surface of sandy substrates, exposing part of the shell (Byrne et al. 1988) and only burrow to shallow depths (McMahon and Bogan 2001). Future experiments examining this behaviour and how it may influence desiccation tolerance as well as different body size/ontogeny classes would be of considerable value to advance our knowledge on this highly successful invasive species.

Devising safe and effective measures to control or eradicate bio-fouling organisms such as Asian clams represents a challenge for applied ecologists and environmental managers. For instance, McDowell et al. (2017) observed that over 99% of *Corbicula* were eliminated by immersion in water at 40 °C for 90 s. Although the ability to achieve this under field conditions is unrealistic. Oxygen depletion and impermeable benthic barriers have produced promising results in the control of *C. fluminea* populations in Lake Tahoe (USA—Wittmann et al. 2012) and pelleted dry ice has been successfully utilised in Ireland on both submerged and emerged clams in laboratory trials (Coughlan et al. 2018). Dewatering and desiccation events have been proposed as potential alternatives to chemical control measures (especially given that no chemical products or impermeable infrastructure is required) in some situations for *D. polymorpha* (Paukstis et al. 1999). For instance, it has been suggested that aerial exposure (at temperatures > 20 °C) may be an effective control of zebra mussels in highly regulated waterways where water levels can be reduced for more than 24 h (Paukstis et al. 1999). In the current study, periods of 24 h with sustained air temperatures of around 25 and 30 °C eliminated 90% of individuals and has the potential to be used to control the spread of *C. fluminea*. However,

more realistically, an extended period of at least 5–6 days would be required to reach similar mortality levels (90%) at an air temperature of 15 °C (Tables 2-3) for the population in the current study.

Our findings on the temperature implications, size classes, lethal temperatures and duration times provides valuable information on the effect of desiccation and air temperature on the mortality of *C. fluminea*. This is of auto-ecology interest and could be used by environmental managers for developing strategies (e.g., dewatering and water level management) for the control of this invasive species. These findings may also be useful as starting point for the development of specific protocols and tests (e.g. required number of days of air exposure for different temperature conditions) to avoid their spread via recreational boats and other submerged objects that may be transferred between waterbodies. When considering the potential wider indirect effects on aquatic ecosystems, proposed techniques to control the spread of *C. fluminea* (e.g., management of desiccation events, oxygen depletion or chemical treatments) should only be applied in heavily modified systems (i.e. with limited conservation interest) and after pilot studies. Artificial waterways, irrigation structures, pipes, cooling systems and power stations where *C. fluminea* establish populations would be suitable systems for the deployment of dewatering and desiccation measures as they could form part of routine management practices to prevent their wider dispersal into surrounding waterbodies.

Compliance with ethical standards

Conflict of interest The authors declare that they have no potential conflict of interest in relation to the study in this paper.

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