Population structure and microhabitat preference of a threatened freshwater mussel, *Westralunio carteri*, in south-western Australia

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Abstract Freshwater mussels are important functional components of aquatic ecosystems. *Westralunio carteri* is a threatened freshwater mussel species, endemic to south-western Australia, which has suffered a recent, dramatic decline in range. The density, size structure and distribution of adult mussels of this species within river reaches were investigated using quadrat searches and modelled against a range of microhabitat factors. Mussels were found from 26 sites in 14 different rivers at a mean density of 28.4 ± 2.3 individuals m⁻². The distribution of *W. carteri* was highly aggregated within river reaches. The most important factors explaining mussel distribution were substrate grain size, substrate debris and distance from the riverbank, with finer substrate, the presence of woody debris and proximity to the riverbank associated with greater abundance of mussels. In all rivers where mussels were found, most populations appeared to be actively recruiting. However, no mussels were found in six sites, despite them having been recorded as present within the last 20 years, which suggests that the range of the species is still in decline. The identification of microhabitat requirements for *W. carteri* will assist in identifying suitable release sites for translocation and/or captive propagation, which may be required to prevent extinction of the species.

Keywords Unionida · Density · Distribution · Aggregation · Fine sediment · Conservation

Introduction

Freshwater mussels (Bivalvia: Unionida) perform a range of important functions in aquatic ecosystems (Vaughn & Hakenkamp, 2001; Strayer, 2008; Vaughn, 2018). Their filter-feeding activity removes phytoplankton, bacteria and particulate matter from the water column, improving water quality and decreasing the likelihood of detrimental algal blooms (Caraco et al., 2006; Nam et al., 2015; Chowdhury et al., 2016). Freshwater mussels are also key habitat couplers, transferring energy and nutrients from pelagic to benthic zones, thereby increasing the diversity and abundance of meiofauna (Howard & Cuffey, 2006; Vaughn & Spooner, 2006; McCasker & Humphries, 2021). In addition, mussels provide food for a variety of predators, including mammals, birds, reptiles and fish (Vaughn, 2018), and in both life and death, their shells may be employed as shelters and
refuges by other aquatic organisms (Beckett et al., 1996; Spooner & Vaughn, 2006). Additionally, they can be of economic and cultural value to people, as a source of mother-of-pearl and food (FAO, 2014).

There are currently 958 valid species of freshwater mussels, with representatives across all continents except Antarctica (Graf & Cummings, 2021). Over the last century, however, there has been a dramatic global decline in both species richness and overall abundance, resulting in the Unionida being recognised as one of the most endangered faunal groups in the world (Lopes-Lima et al., 2018; Ferreira-Rodríguez et al., 2019). The global decline of freshwater mussel populations is likely due, in part, to their life-history characteristics, which make them vulnerable to environmental change. Juvenile and adult mussels are relatively sedimentary, increasing their vulnerability to environmental disturbances (Green et al., 1985; Brainwood et al., 2006). Many mussel species are also long-lived (decades to up to 100+ years), with delayed reproduction and long generation times, which limits their capacity to recover from population declines (Galbraith et al., 2010; Haag & Rypel, 2011).

A number of recent papers have addressed research priorities to develop effective conservation strategies for freshwater mussels (e.g. Haag & Williams, 2014; Quinlan et al., 2015a; Lopes-Lima et al., 2018; Ferreira-Rodríguez et al., 2019). Consistently featured among these priorities are knowledge of population demography and an understanding of the environmental factors that determine mussel distribution and abundance. Obtaining demographic data, particularly age structure, is important to ensure that mussel populations are actively recruiting; the long lifespan of mussels means that adult populations can persist after juvenile recruitment has ceased and these relict populations, consisting solely of adult mussels, have been reported for a number of species (e.g. Hanson & Locke, 2001; Österling et al., 2008; Strayer & Malcom, 2012). Knowledge of environmental factors affecting mussel distribution and abundance underpins the development of environmental targets to guide river and catchment management (Quinlan et al., 2015a). A wide range of factors, operating at local habitat, river reach and catchment scales, have been correlated with mussel presence and abundance (Strayer, 2008; Haag, 2012). In particular, a number of studies have emphasised the importance of microhabitat characteristics, such as substrate type, hydrology, in-stream debris and macrophyte cover (e.g. Strayer, 1993; Hastie et al., 2000a; Brim Box et al., 2002; McRae et al., 2004; Cyr et al., 2012).

There are 18 described species of freshwater mussels in Australia, and although there is evidence of declines in abundance or range of a number of species, detailed assessment of conservation status of the Australian mussel fauna has been hampered by inadequate data (Jones & Byrne, 2014; Walker et al., 2014). *Westrallonio carteri* Iredale, 1934 (Hyriidae) is endemic to south-western Australia. It is the only freshwater mussel species currently described from the region, although recent molecular studies have identified distinct, spatially structured genetic lineages and highlighted the need for a taxonomic revision (Klunzinger et al., 2021; Benson et al., 2022). *Westrallonio carteri* (sensu lato) is found only in the South-west Coast Drainage Division of Western Australia, being largely restricted to lotic and lentic systems in forested areas within 100 km of the coast (Klunzinger et al., 2015). It is a slow growing and long-lived species, reaching maturity at 4–6 years and having a maximum age of more than 50 years (Klunzinger et al., 2014). The species is a host-generalist, with glochidia being recorded from seven species of native freshwater fishes and four species of introduced alien fishes (Klunzinger et al., 2012). A combination of increasing salinity, drought and nitrogen-related pollution has led to a 49% decline in its extent of occurrence (EOO) over the past 50 years (Klunzinger et al., 2015), resulting in its classification as Vulnerable on the IUCN Red List (Klunzinger & Walker, 2014) and under both the Australian *Environment Protection and Biodiversity Conservation Act 1999* (Threatened Species Scientific Committee, 2018) and the Western Australian *Biodiversity Conservation Act 2019* (Government of Western Australia, 2018).

While recent studies have clarified many aspects of the biology of *W. carteri* (Klunzinger et al., 2012, 2014, 2015), further information is required to enhance the development and implementation of conservation management plans. Although the current range of *W. carteri* was comprehensively mapped by Klunzinger et al. (2015), this was based almost entirely on presence/absence data; the density, age structure and recruitment status of most extant populations are not known. In addition, while associations of mussel presence with land use and water quality
variables at the river reach scale were investigated by Klunzinger (2012) and Klunzinger et al. (2015), there is no information on microhabitat preferences (sensu Morrison et al., 2012) within a reach. The aim of the current study was to address these knowledge gaps by surveying a number of extant populations of *W. carteri* to estimate: (1) mussel density; (2) pattern of spatial distribution; (3) size/age structure and (4) the relationship between mussel abundance and micro-habitat features.

**Methods**

**Study area**

Recent work has identified the occurrence of two distinct, geographically separated lineages (and putative new species) within the range of the currently described *W. carteri* (Klunzinger et al., 2021; Benson et al., 2022). This study was conducted in the range of the lineage “*W. carteri*” I of Klunzinger et al. (2021), which is found on the west coast of south-western Australia. Thirty-two sites from 17 rivers (Fig. 1) in the South-west Coast Drainage Division of Australia were selected based on recently recorded occurrence data (Klunzinger et al., 2015). All sampling occurred over a 2-year period between late summer and early winter (February–June), when water flow is lowest. Each site was surveyed only once throughout the sampling period, and the location of each sampling site was recorded by Garmin® Etrex30 GPS handset. As sites within rivers were not separated by barriers to fish movement, we refer to the mussels within each site as a subpopulation and the mussels from all sampled sites within the same river as a population.

**Mussel sampling**

At each site, three to five transects (depending on accessibility) were selected haphazardly across the width of the channel, approximately 5 m apart. At each transect, between 2 and 10 quadrats were taken from bank to bank, the number depending on the width of the channel. Quadrat sampling is the preferred method for estimating density and distribution of mussels in wadeable streams (Obermeyer, 1998; Strayer & Smith, 2003). We used 25 × 25 cm quadrats (area 625 cm²), a standard sampling unit size for freshwater mussels (e.g. Hastie et al., 2000a; Brim Box et al., 2002; Smith et al., 2003; Jones, 2007; Ostrovsky & Popov, 2011). Each quadrat was searched systematically by hand, to a depth of approximately 10 cm, until no new mussels were found. Mussels in each quadrat were counted and measured for total shell length (TL) (McMichael & Hiscock, 1958) with Vernier calipers to the nearest 0.1 mm and then returned to their original location.

**Microhabitat variables**

A range of microhabitat variables that have been found to influence abundance in other freshwater bivalve species (e.g. Hastie et al., 2000a; Johnson & Brown, 2000; Dittman et al., 2018) were measured for each quadrat: distance from quadrat centre to the riverbank; water depth; riverbed slope; current velocity; substrate grain size; the presence of woody debris; debris height; percentage cover of macrophytes; percentage cover of algae and percentage cover of total vegetation (macrophytes, algae and other plant material, such as leaf litter) (Table 1). Distance to riverbank and water depth were measured with a tape measure to the nearest 5 cm. Riverbed slope was measured using an Empire™ Magnetic POLYCAST® protractor to the nearest 1°. Substrate grain size was calculated using the particle size index of Strayer (1999). Briefly, the percentage cover of 10 sediment types (silt, clay, earth, sand, coarse sand, peat, gravel/pebble, cobble, boulder and rock) following Raven et al. (1998) was estimated subjectively, each sediment type was assigned a value from 1 to 10 in order of increasing grain size, and a weighted average calculated for each quadrat. Debris height was measured with a ruler to the nearest 0.5 cm. All percentage cover values (i.e. sediment type, macrophytes, algae and total vegetation) were estimated by visual inspection and recorded in increments of 5%.

**Data analysis**

Shell length–frequency data were plotted for all populations where at least 20 mussels were measured. Klunzinger et al. (2014) validated shell ring annuli for *W. carteri*, but these cannot be measured reliably on living animals (i.e. without sectioning the shell). To estimate age of mussels, the age at length curves calculated by Klunzinger et al. (2014) for five
Microhabitat preference, defined as a statistical description of habitat use relative to availability in the field (Beyer et al., 2010; Morrison et al., 2012), was analysed using generalised linear models (GLMs) in R (R Core Team, 2021), with number of mussels per quadrat (referred to here as abundance) as the response and microhabitat variables as predictors. Prior to analysis, correlations among continuous microhabitat variables were examined and significant correlations were found between distance to riverbank and water depth, and between percentage vegetation cover and both percentage macrophyte cover and percentage algae cover. To reduce collinearity among predictors, and to minimise over-fitting during model construction, water depth, macrophyte cover and algae cover were removed from the variable set. This left seven, largely independent microhabitat predictors (all pairwise correlations between continuous predictors < 0.3, Table 2).

As mussels were aggregated in space and there were many quadrats which contained no mussels (see “Results” section), mussel distribution was modelled as both a negative binomial and a zero-inflated negative binomial, using the R packages MASS (Ripley et al., 2018) and pscl (Jackman, 2020). Neither model showed evidence of overdispersion (ratio of residual deviance to residual degrees of freedom less than two, and dispersion parameter close to one in both cases), and there was little difference between the models in normal QQ plots, or in AIC or BIC values. Zero-inflated models assume that excess zeros are generated by a separate process from count data and are therefore modelled separately. Because this analysis was restricted to localities that contained mussel populations on a reach scale (i.e. there was never a zero probability of mussels being present in a quadrat in the selected reach), the negative binomial model was considered more appropriate and is presented here.

A multi-model inference approach was employed to determine the relative importance of microhabitat variables in explaining mussel distribution. First, a global GLM was fit in MASS using all seven non-correlated predictors. The global model was used to generate a set of all possible models using the R package MuMIn (Bartoń, 2020). Models were ranked by their AIC value and model averaging performed across all models within four AIC values of the best model. The importance of each variable was measured as the proportional occurrence of that variable...
across all models within the top ranked set, and the significance of model-averaged coefficients was determined with a z-test. Locality was not included in the global model because it prevented convergence. Instead, to check that the effect of microhabitat predictors was independent of the river from which quadrat samples were obtained, we ran a reduced generalised linear mixed model (GLMM) using the R package lme4 (Bates et al., 2015), including river as a random effect and only those predictors which were significant ($P < 0.05$) from model averaging and had an importance greater than 0.90.

### Results

A total of 875 mussels were recorded from 26 sites in 14 rivers (Fig. 1). No mussels were found in a further six sites; three in rivers from which mussels were found at other localities and three in rivers from which no other localities were sampled. Klunzinger et al. (2015) had previously recorded mussels as present in all sampled sites, based on occurrence records from 1992 to 2012. Channel width at sites where mussels were found ranged from 2 to 25 m (mean = 9.18 ± SE 0.79 m), with relatively narrower water width, ranging from 0.6 to 15 m (6.02 ± 0.51 m).

#### Table 1 Predictor variables for modelling the habitat preference of *Westralunio carteri*

| Variable names                      | Type            | Measurement       | Mean ± SE | Range |
|-------------------------------------|-----------------|-------------------|-----------|-------|
| Distance to riverbank               | Continuous      | m                  | 0.98 ± 0.04 | 0–3.88 |
| Water depth                         | Continuous      | m                  | 0.26 ± 0.01 | 0.02–0.92 |
| Streambed slope                     | Continuous      | Degrees            | 7.8 ± 0.3  | 0–49.0 |
| Debris presence                     | Categorical     | Yes, no            | N/A       | N/A   |
| Debris height                       | Continuous      | cm                 | 3.7 ± 0.34  | 0.1–116.0 |
| Flow velocity                       | Continuous      | m s$^{-1}$         | 0.05 ± 0.01 | 0–1.00 |
| Substrate grain size                | Continuous      | Grain size index   | 2.7 ± 0.1  | 1.0–10.1 |
| Macrophytes                         | Continuous      | %                  | 12.8 ± 1.4 | 0–100 |
| Algae cover                         | Continuous      | %                  | 16.3 ± 1.5 | 0–100 |
| Vegetation cover                    | Continuous      | %                  | 31.8 ± 1.8 | 0–100 |

#### Table 2 Correlations among continuous predictor variables for modelling the habitat preference of *Westralunio carteri*

| BD | WD | BS | DH | FV | SG | VC | MC | AC |
|----|----|----|----|----|----|----|----|----|
| 0.47 | 0.16 | 0.03 | 0.07 | 0.09 | 0.06 | 0.16 | 0.02 |
|   | 0.16 | 0.06 | 0.07 | 0.15 | 0.10 | 0.10 | 0.17 |
|   | 0.00 | 0.13 | 0.01 | 0.01 | 0.07 | 0.17 | 0.02 |
|   | 0.11 | 0.10 | 0.06 | 0.09 | 0.05 | 0.10 | 0.16 |
|   | 0.04 | 0.04 | 0.01 | 0.04 | 0.02 |    |    |
| VC | 0.57 | 0.66 |    |    |    |    |    |
| MC |   |    |    |    |    |    | 0.10 |

Significant correlations ($P < 0.05$) in bold

*BD* distance to riverbank, *WD* water depth, *BS* riverbed slope, *DH* debris height, *FV* flow velocity, *SG* substrate grain size, *VC* vegetation cover, *MC* macrophyte cover, *AC* Algae cover

For analysis of population structure, sites in the same river were combined. Over all river populations, TL of sampled mussels ranged from 18.95 to 95.60 mm (mean = 63.43 ± SE 0.39 mm, Fig. 2). Using size at age estimates from Klunzinger et al. (2014), this corresponds to an age range of approximately 20–40 years.
1.5–62.5 years, with the majority of mussels aged between 10 and 20 years (Fig. 3). There were differences among populations in size distribution, with Yalyal Brook, Helena River and Serpentine River having a much greater number of larger, older mussels (Figs. 2, 3). Juvenile mussels (TL < 31.5 mm) were rarely found (only two juveniles in two rivers). However, all populations except one (Helena
River) showed some evidence of recent recruitment (i.e. mussels aged 10 years or less). Recruitment index (proportion of mussels ≤ 10 years) varied significantly among rivers ($\chi^2_{11} = 146.70; P < 0.0001$), with a range from 0.01 to 0.74 (mean = $0.22 \pm$ SE 0.06).
Density and distribution

Mean mussel density per site ranged from 3.2 (95% CI = 0–6.4) to 106.0 (95% CI = 43.7–212.0) individuals m⁻² (density estimates for all sites are shown in Supplementary Information, Table S1). Over all sites, the mean density was 28.5 (95% CI = 24.3–33.7) individuals m⁻². The species had an aggregated distribution within populations, approximating a negative binomial with $k = 0.47$ (observed values not significantly different from expected by $\chi^2$ test, $P = 0.720$). The variance to mean ratio was 5.96 (95% CI 4.28–9.08) and Lloyd’s IP was 3.79 (95% CI 3.04–5.19) ($\chi^2$ test of departure from randomness, $P < 0.001$). The distribution remained aggregated even when quadrats without mussels were removed from the analysis (variance:mean ratio = 4.41, 95% CI 3.05–7.00; IP = 2.03, 95% CI 1.61–2.70, $\chi^2$ test $P < 0.001$).

Habitat preference

The global GLM for mussel abundance, using all seven predictor variables, had a residual deviance of 498 on 478 degrees of freedom and a dispersion parameter of 0.55, indicating that no correction was necessary for overdispersion. Substrate grain size and distance to the riverbank were the most important predictors of mussel abundance, occurring in all the top AIC models and with the model-averaged coefficients being statistically significant (Table 3). The only other variable which occurred in more than 50% of models was the presence of debris, occurring in 95% of the top AIC models and with a significant model-averaged coefficient ($P = 0.027$). When river was included as a random effect in a reduced GLMM, all fixed effects remained significant (for substrate grain size, $z = -4.09$, $P < 0.001$; the presence of debris, $z = 2.22$, $P = 0.026$; distance to the riverbank, $z = -2.11$, $P = 0.041$). Higher mussel abundance was associated with quadrats that had finer substrate, contained woody debris and were closer to the riverbank (Fig. 4).

Discussion

*Westralunio carteri*, the only formally recognised freshwater mussel species in south-western Australia, has undergone a severe decline in range over the last 50 years (Klunzinger et al., 2015). Although the current range of the species has been mapped and the principal environmental threats identified (Klunzinger et al., 2015), this is the first investigation of the age structure, density, fine-scale distribution and microhabitat preference of remaining extant populations of *W. carteri*. For almost all rivers in which mussels were present, there was evidence of recent recruitment and mussel density was relatively high. Within river reaches, mussels had an aggregated distribution and mussel abundance was positively related to finer grained substrates, the presence of woody debris and proximity to the riverbank. These findings have important implications for the conservation management of this threatened species.

Alarmingly, mussels were found in only 81% of examined sites, despite the sample sites being chosen from a database of recent (1992–2012) occurrence records. This is not necessarily an indication of recent extinction of these subpopulations; previous

### Table 3 Association between habitat variables and abundance of *W. carteri* in quadrat samples

| Microhabitat variable       | Importance | Est. coefficient (± SE)   | $z$ Value | Pr (>|$z$|) |
|----------------------------|------------|---------------------------|-----------|----------|
| Substrate grain size       | 1.00       | $-0.184$ (± 0.041)        | $-4.46$   | $< 0.001$|
| Distance to riverbank      | 1.00       | $-0.243$ (± 0.100)        | $-2.43$   | 0.015    |
| Debris presence—Yes        | 0.94       | $0.548$ (± 0.247)         | 2.21      | 0.027    |
| Debris height              | 0.53       | 0.011 (± 0.009)           | 1.30      | 0.192    |
| Vegetation cover           | 0.38       | $-0.002$ (± 0.002)        | $-0.98$   | 0.325    |
| Riverbed slope             | 0.28       | 0.007 (± 0.010)           | 0.65      | 0.558    |
| Current flow velocity      | 0.23       | $-0.031$ (± 0.803)        | $-0.04$   | 0.970    |

Variables are ranked by relative importance (probability of selection in AIC best-fit models), with coefficient estimates and standard errors from model averaging. Significant predictors ($P < 0.05$) are shown in bold.
Fig. 4 Relationship between mussel abundance (number per quadrat) and environmental predictors: A substrate grain size (size index—see “Methods” section), B presence of debris (N = No; Y = Yes), and C distance to riverbank (m).
occurrence records provided no information on population size, so it may be that mussel density was very low and transect sampling in this study simply did not locate them. Nevertheless, given the current listing of the species as Vulnerable, the absence of mussels at almost 20% of sites in this study is of concern. Although no obvious environmental impacts were found to explain the loss of subpopulations, this was not investigated in any detail and there is a need to revisit these sites for more intensive study. We note that similar declines of other freshwater species have occurred across this same region over a similar timeframe (Morgan et al., 2014; Ogston et al., 2016), and this reinforces the need for further research.

Size/age structure

An encouraging finding from this study was evidence of recent recruitment in most rivers. Although sediments in each quadrat were searched by hand to locate mussels, this was unlikely to detect juvenile mussels (defined here as TL < 31.5 mm) and these were probably under-represented in the samples (only two juvenile mussels over all populations). This is not surprising because juvenile freshwater mussels are often difficult to detect by standard hand sampling techniques (Strayer & Smith, 2003). This is partly due to their small size, but also to a propensity to burrow deeper into the substrate (Hastie et al., 2000b), and in many cases, they have different habitat requirements to adult mussels (Neves & Widlak, 1987; Morales et al., 2006). In addition, most freshwater mussel species are long-lived, and the juvenile phase represents only a very small component of the lifespan, so they are expected to have a relatively low abundance when hand sampling in most populations (Strayer & Smith, 2003).

The proportion of young mussels (defined here as those with TL < 54 mm, approximately equivalent to <10 years of age, although we recognise that growth rate can vary among populations; Klunzinger et al., 2014) may represent a better measure of recruitment success. By this measure, in almost all rivers where mussels were present, populations appeared to be actively recruiting, although there were substantial differences among populations, with between 1 and 74% of the population in this age bracket. The data from this study were not suitable to investigate the reasons for differences in recruitment index among populations, but this is the focus of ongoing research. Studies of the age structure of freshwater mussel populations are relatively rare, but where they have been carried out, the distributions are frequently right skewed, which might reflect unionid longevity and higher mortality rates in juvenile mussels (Österling et al., 2010; Strayer & Malcom, 2012).

Density and distribution

The mean density over all 32 sites from which W. carteri was sampled in this study was approximately 29 individuals m\(^{-2}\), with mean density within sites ranging from 3.2 to 106.0 individuals m\(^{-2}\). Previous studies in the Northern Hemisphere have found great variability in the density of freshwater mussels, both within and among species, with estimates ranging from much less than one to more than 1,000 individuals m\(^{-2}\) (e.g. James, 1985; Downing & Downing, 1992; Hastie et al., 2000b; Zigler et al., 2008; Ostrovsky & Popov, 2011; Annie et al., 2013; Chowdhury et al., 2016). There have been only limited previous estimates of population densities among Australian Hyriidae: Walker (1981) reported 1.2 individuals m\(^{-2}\) for Alathyria jacksoni Iredale, 1934 and 3.7 m\(^{-2}\) for Velesunio ambiguus (Philippi, 1847) in the Murray River, South Australia; Humphrey (1984) found a maximum density of 18.2 individuals m\(^{-2}\) for Velesunio angasi (Sowerby, 1867) in Magela Creek, Northern Territory; Jones (2007) recorded densities ranging from <0.001 to 36.7 individuals m\(^{-2}\) for A. jacksoni and <0.001 to 0.04 m\(^{-2}\) for V. ambiguus in the Barwon-Darling River system in New South Wales; and Brainwood et al. (2008) found a mean of 50 individuals m\(^{-2}\) in mixed species assemblages (V. ambiguus, Hyridella australis (Lamarck, 1819) and Hyridella depressa (Lamarck, 1819)) in the Hawkesbury-Nepean River in New South Wales.

Westralunio carteri had a strongly aggregated distribution within populations. This is not uncommon in freshwater mussels (Neves & Widlak, 1987; Downing & Downing, 1992; Downing et al., 1993; Hastie et al., 2000a), although a random distribution has been reported in some species (Cyr et al., 2012) and patterns of dispersion may differ among populations of the same species and temporally in the same population (Downing & Downing, 1992; Perles et al., 2003; Zieritz et al., 2014). There are a number of (not mutually exclusive) explanations for aggregation.
in freshwater mussel populations. Aggregation on the stream bed might be simply a by-product of the aggregation of glochidia among fish hosts, which has been previously reported for *W. carteri* (Klunzinger et al., 2012) and is an almost universal feature of macroparasite/host relationships; or of non-random spatial variation in the survival of juvenile mussels, once they detach from the host (Hansen & Larsen, 2005; Verween et al., 2007; Terui & Miyazaki, 2015). Alternatively, aggregation may be an adaptation, for example, for protection (Hopper et al., 2019) or to enhance reproductive success. Downing et al. (1993) found a strong relationship between aggregation and fertility in *Elliptio complanata* (Lightfoot, 1786) and aggregation has been found to increase during spawning periods in a number of species (Amyot & Downing, 1998; Zieritz et al., 2014). Aggregation may also arise if juvenile or adult mussels exhibit habitat selection and selected habitats are spatially discontinuous (Perles et al., 2003).

Habitat preference

The distribution of freshwater mussel species is likely to be influenced by a number of different factors operating over a range of ecological scales (Strayer, 2008). In this study, we examined microhabitat features at a local scale within river reaches and found that substrate grain size, the presence of woody debris and distance from the riverbank were associated with mussel abundance. More mussels were found on fine sediments, in association with woody debris and close to the riverbank. It should be noted, however, that the absence of “good” environmental characteristics that predict mussel density does not preclude the presence of *W. carteri*, with individuals also occasionally found in rocky, relatively bare riverbeds, as has been shown in other species across the world (Brainwood et al., 2008; Smith & Meyer, 2010).

Several previous studies have found substrate grain size to be an important predictor of mussel abundance, although in contrast to our results, most have reported an apparent preference for coarser substrates (James, 1985; Neves & Widlak, 1987; Hastie et al., 2000a; Johnson & Brown, 2000; Brainwood et al., 2008). These studies have generally been in large rivers with permanent water flow and it is usually assumed that the preference for coarser substrates arises because larger particles, such as coarse sand and cobbles, promote stream bed stability (Johnson & Brown, 2000; Quinlan et al., 2015a). Stream bed scouring associated with flood events can be a major source of mortality for freshwater mussels (Vannote & Minshall, 1982; Hastie et al., 2001; Morales et al., 2006). However, south-western Australia, like many other areas of the world with arid or Mediterranean climates, is characterised by relatively small, non-perennial river systems, which cease to flow in the dry season and are often reduced to a number of disconnected refuge pools (Beatty et al., 2017). Flooding events are rare and benthic stability may not be a major habitat requirement in these systems.

Far fewer studies have reported an association of mussel abundance with smaller substrate grain size, although Brim Box et al. (2002) found that *Villosa lienosa* (Conrad, 1834) was most common in substrates with a high proportion of fine sediments. Finer substrates, such as silt, may contain more organic matter as a food source for filter-feeding mussels (Lara & Parada, 2009), although silt is also considered to be detrimental to feeding and respiratory activity in mussels (Roper & Hickey, 1995; Brim Box & Mossa, 1999). A more likely explanation for a preference for finer substrates may be that they enhance burrowing efficiency (Lewis & Riebel, 1984; Morales et al., 2006; Poznańska-Kakareko et al., 2021; although see Hyväri (2021) for a contrary finding with juvenile mussels). Burrowing may provide protection against drought (Amyot & Downing, 1997; Gough et al., 2012), which would be an important adaptation in regions with non-perennial rivers, such as south-western Australia, where river drying is a regular annual occurrence. Lymbery et al. (2021) found that burrowing significantly reduced the mortality rate of *W. carteri* during water emersion, with burrowed mussels able to survive at least 62 days out of water.

Associations between mussel abundance and substrate grain size may be more complex than a simple preference for coarse or fine sediments. There is evidence that *Margaritifera margaritifera* (Linnaeus, 1758), for example, may occur more frequently in habitats with particular grain size distributions, i.e. mixtures of sediments with different grain sizes (Quinlan et al., 2015a). In addition, a number of studies have found juvenile and adult mussels of the same species may have different habitat preferences in the
field (Hastie et al., 2000a, b; Annie et al., 2013). We did not investigate the effect of grain size variability on the abundance of *W. carteri*, or whether grain size preference differed between adults and juveniles, but these will be important topics for future study.

In addition to the association with finer substrates, there was also evidence from our study that mussel abundance was greater in the presence of woody debris and closer to the riverbank. This may suggest avoidance of rapid water flow, as previous studies with other species have found that mussel abundance is often greatest in flow refuges, such as channel banks and border areas, amongst root-mats and the downstream side of boulders, logs and large woody debris (Neves & Widlak, 1987; Strayer, 1999; Howard & Cuffey, 2003; Zigler et al., 2008). This apparent preference for flow refuges is usually considered an adaptation to prevent mussels being swept away (Strayer, 1999; Maloney et al., 2012), although areas of low flow may also provide a better food source for filter feeders such as mussels (Morales et al., 2006). Proximity to riverbanks may also be a hypoxia-avoidance strategy, with deeper habitats more likely to contain reduced dissolved-oxygen saturations, as a result of water column stratification (Quinlan et al., 2015b).

Habitat preference, as measured by associations between mussel abundance and habitat features in the field, does not necessarily indicate active habitat selection, as it could arise through a random distribution on settling, followed by differential mortality in habitats of different suitability. Although freshwater mussels are often regarded as relatively sessile organisms, Lymberry et al. (2021) found that *W. carteri* could move up to 85 cm in 3 days to track retreating water levels, and movement rates of up to 60 cm day$^{-1}$ have been recorded in other species (e.g. Amyot & Downing, 1997, 1998; Schwab & Pusch, 2007; Gough et al., 2012; Daniel & Brown, 2014). This suggests that active habitat selection is possible and, indeed, this has been demonstrated in laboratory experiments for several mussel species. For example, a predilection for fine over coarse substrates has been found in choice experiments with *Lampsilis radiata* (Gmelin, 1791) (Huehner, 1987) and *Alasmidonta heterodon* (Lea, 1829) (Michaelson & Neves, 1995). During the current study, extensive tracks left by *W. carteri* on stream beds were frequently observed and these may be related to habitat selection. A controlled laboratory test of habitat selection is an important future research requirement to definitively identify the microhabitat features that are optimal for survival of *W. carteri*.

Although we have identified several microhabitat features that are associated with the density of *W. carteri*, there are undoubtedly other factors also involved in determining the distribution and abundance of this species. Studies in other freshwater mussel species have emphasised the importance of reach and catchment-scale variables such as land use, geomorphology, stream size and gradient, structure of riparian vegetation, host fish community and water quality parameters (Morris & Corkum, 1996; Vaughn & Taylor, 2000; McRae et al., 2004; Brainwood et al., 2008). Klunzinger et al. (2015) identified water salinity, water permanence and total nitrogen concentration as important reach-scale determinants of the presence of *W. carteri*. There may also be interactions between environmental factors operating at different scales. Brainwood et al. (2008), for example, found that associations between mussel abundance and substrate types in the Hawkesbury-Nepean River differed among reaches with different geomorphological characteristics. This is an area that deserves further study for a more complete understanding of the habitat requirements of *W. carteri*.

Implications for conservation

Freshwater ecosystems cover less than 1% of the surface of the Earth yet contain almost 10% of global animal biodiversity (Dudgeon, 2019). Unfortunately, however, freshwater ecosystems also contain a much greater percentage of threatened species than terrestrial or marine ecosystems, with an average rate of decline of freshwater populations of more than 80% since 1970 (Harrison et al., 2018). The protection of freshwater species, especially those such as freshwater mussels which play key roles in maintaining ecosystem function (Vaughn, 2018), should therefore be a global conservation priority.

Klunzinger et al. (2015) used contemporary and historical presence/absence data to infer that the range of *W. carteri*, the only currently described freshwater mussel species in south-western Australia, had declined by 49% over the last 50 years, resulting in an assessment as ‘Vulnerable’ by international, national and State agencies. We revisited 32 sites that were reported as containing mussels in surveys between
1992 and 2012 (Klunzinger et al., 2015), and could not find mussels at 19% of these sites; this suggests that population declines are still occurring, although it is possible that mussels were present, but at very low densities. In any case, given the projected reductions in rainfall and streamflow as a result of climate change in south-western Australia (Silberstein et al., 2012; Andrys et al., 2017), it is likely that active interventions, such as translocation and captive propagation, will be necessary to conserve the species. From this viewpoint, the evidence of active recruitment in most of the remaining populations that were surveyed is encouraging, as these will be needed as a source of re-establishment. In addition, understanding the habitat requirements, particularly the preference for finer sediments, is important to identify suitable release sites for translocation and captive breeding schemes (Moorkens, 2018). The presence of suitable habitat for burrowing during water emersion is likely to be a key requirement for population survival as the frequency and length of droughts continue to increase throughout southern Australia.

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Data availability Data from this study have been deposited with Mendeley (https://www.data.mendeley.com/drafts/frkvyhmz2). Coordinates for sampling locations are available from the corresponding author, upon reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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