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RESEARCH ARTICLE

Effects of translocation on survival and growth of freshwater mussels within a West Gulf Coastal Plain river system

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Abstract

1. Human-mediated threats have led to the rapid decline of species inhabiting freshwater ecosystems, and among the groups most affected are freshwater mussels of the family Unionidae. As a result, species translocation is increasingly used in conservation programmes, yet experimental evidence documenting the success of this strategy is limited.
2. The goal of this study was to examine the effects of translocation on survival probability, shell growth and body condition of a state-threatened (*Quadrula houstonensis*) and common (*Amblema plicata*) species of freshwater mussel in the San Saba River, located in a West Gulf Coastal Plain river system, USA.
3. Survival probability estimated from a joint live and dead encounter model was high (> 0.85) and varied by treatment for both species. However, differences in survival probability between resident and transplant treatments were relatively small for *A. plicata* (0.01) and *Q. houstonensis* (0.12). Generalized additive mixed models of yearly proportional growth and linear mixed models of Fulton's K index for *A. plicata* varied by treatment and were lower in transplant treatments. Shell growth of *Q. houstonensis* was unaffected by translocation; whereas, Fulton's K was higher in the transplant treatment.
4. Methods used to translocate mussels were important factors leading to high survival and limited impacts to shell growth and body condition in this study. Differences in shell growth rate between treatments are attributed to possible differences in habitat quality between sites.
5. Our results demonstrate that *A. plicata* and *Q. houstonensis* are tolerant of translocation, despite the broad assumption that translocation is detrimental to mussels. Thus, there is a continuing need to study species' responses to translocation to test and improve the ecological soundness of this strategy, particularly because climate change and other human stressors will exacerbate the need to implement conservation measures such as translocation in future decades.

KEYWORDS

invertebrates, protected species, river, species recovery, translocation, unionids

1 | INTRODUCTION

Human-mediated threats to the environment have led to the global decline of species diversity in freshwater ecosystems (Dudgeon et al., 2006; Strayer & Dudgeon, 2010). In lotic ecosystems, there are several major categories of impacts that have fundamentally transformed rivers and driven species declines, including over-exploitation, pollution, alteration of natural flow regimes (e.g. via dams), invasive species, destruction and fragmentation of habitat and climate change (Allan & Flecker, 1993; Strayer & Dudgeon, 2010). Consequently, conservation tools such as translocation – the process of moving and establishing populations from one location to another (IUCN/SSC, 2013) – are used increasingly in mitigation of biodiversity loss and maintenance of ecosystem function (Armstrong & Seddon, 2008; Chauvenet, Ewen, Armstrong, Blackburn, & Pettorelli, 2013; Olden, Kennard, Lawler, & Poff, 2011). However, while studies suggest that the success of translocation has been low (Fischer & Lindenmayer, 2000; Griffith, Scott, Carpenter, & Reed, 1989; Massei, Quy, Gurney, & Cowan, 2010), leading some to question the merits of this method, the viability of translocation as a conservation strategy has not been thoroughly evaluated; in part, because of the lack of experimental evidence and absence of rigorous protocols for some taxonomic groups (Fischer & Lindenmayer, 2000).

Freshwater mussels of the family Unionidae are sedentary, filter-feeding bivalves that represent one of the most endangered groups of aquatic taxa worldwide (Lydeard et al., 2004), yet efforts to mitigate their endangerment are being outpaced by the rapid decline of mussel diversity (Haag & Williams, 2014; Lopes-Lima et al., 2014). Impacts to mussels have been attributed to human alterations of freshwater ecosystems, coupled with several life-history traits that render mussels vulnerable to disturbances, including limited mobility, long generation times and dependence on fishes to complete their life cycle (Downing, Van Meter, & Woolnough, 2010; Vaughn & Taylor, 1999). The imperilment of this group is of growing concern because mussels provide important ecosystem services to inland waters (Vaughn, 2010; Vaughn & Hakenkamp, 2001), including functioning as biomonitors of pollution (Gustafson, Showers, Kwak, Levine, & Stoskopf, 2007), enhancing nutrient cycling and trophic interactions in aquatic communities (Allen, Vaughn, Kelly, Cooper, & Engel, 2012; Vaughn, 2010; Vaughn, Spooner, Galbraith, & Vaughn, 2007) and increasing habitat diversity in benthic environments (Spooner & Vaughn, 2008).

Translocation of freshwater mussels is commonly used to move individuals in response to in-stream construction activities (Cope & Waller, 1995; Haag & Williams, 2014; Peck, Harris, Farris, & Christian, 2014), but it has also been used to reintroduce species, augment existing populations or temporarily hold populations in artificial refugia (e.g. hatcheries) (Cope & Waller, 1995; Haag & Williams, 2014; Peck et al., 2014). Despite its frequent use, empirical support for translocation is fairly limited (Cope & Waller, 1995); and consequently, some conservation scientists question the usefulness of mussel translocation (Haag & Williams, 2014). However, the limited success in previous mussel translocations can be attributed to biased mark–recapture techniques (Meador, Peterson, & Wisniewski, 2011; Villella, Smith, & Lemarié, 2004), the inability to identify suitable mussel habitat (Cope et al., 2003; Dunn, Sietman, & Kelner, 1999; Hamilton, Brim Box, & Dorasio, 1997) and inadequate handling and transport procedures (Dunn et al., 1999; Waller, Gutreuter, & Rach, 1999; Yusufzai, Singh, & Shirdhankar, 2010). In addition to these methodological problems, relatively little attention has been given towards assessing whether translocation affects physiological health, growth and reproductive success (Bolden & Brown, 2002; Kesler, Newton, & Green, 2007; Newton et al., 2001; Peck, 2010; Peck et al., 2014; Roznere, Watters, Wolfe, & Daly, 2017), which can have population-level consequences. Therefore, lack of in-depth study of mussel translocation has prevented its use for other conservation purposes, such as facilitating gene flow among fragmented populations (Galbraith, Zanatta, & Wilson, 2015; Weeks et al., 2011) or transplanting populations in response to climate change (Olden et al., 2011).

The west Gulf Coastal Plain region, ranging from the Brazos River, Texas west to the Rio Grande River, New Mexico, contains a unique assemblage of freshwater mussels comprising at least 31 described species, 11 of which are endemic to this region (Haag, 2010; Howells, Neck, & Murray, 1996). Human population growth is expected to double in this region by 2050 (Potter & Hoque, 2014) and climate models predict increased drying and higher frequency of multi-year droughts throughout the region (Seager, 2007), which in turn will increase demand for water resources and threaten aquatic faunas (Packard, Gordon, & Clarks, 2011). In fact, population reduction and range contraction for some mussel species has already warranted protection under local state (Texas and New Mexico) and US federal laws (Endangered Species Act, ESA) (Carman, 2007; TSS (Texas Secretary of State), 2010; USFWS (U.S. Fish and Wildlife Service), 2011). Given these concerns, traditional strategies to protect mussels (e.g. habitat restoration) may be insufficient in future decades, and conservation tools such as translocation may become increasingly needed, particularly for moving populations outside historic ranges in response to rising temperatures and drought associated with climate change (Olden et al., 2011). However, only relatively few species across disparate regions have been tested for the ecological soundness of translocation as a conservation tool. The objective of this study was to examine the effects of translocation on freshwater mussels, particularly mussel species occurring in the West Gulf Coastal Plain region of the United States. The specific goals of this study were to test the effects of translocation on survival probability, shell growth and body condition of both common and rare species in the San Saba River, Texas.

2 | METHODS

2.1 | Site and species selection

The effects of translocation on freshwater mussels was studied in the San Saba River, a tributary of the Colorado River, Texas located in the West Gulf Coastal Plain region of south-central USA (Figure 1). The San Saba River is surrounded by the Montane ecoregion with uplands of limestone bedrock, relatively little soil cover and semiarid to subtropical–subhumid climate (Blum, Toomey, & Valastro, 1994). Two sites within the lower San Saba River, which are part of a larger

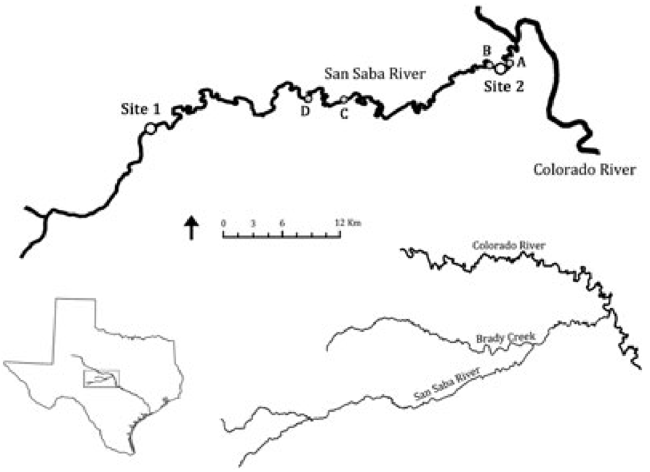

FIGURE 1 Map of the two relocation sites (sites 1 and 2, white points) and four relocation sites initially examined for suitability of translocation (sites A–D, grey points)

ongoing study in the river, were selected for translocation based on the following criteria: (1) population and assemblage characteristics (i.e. abundance, species richness and evidence of recent recruitment) and suitable mussel refugia (Cope et al., 2003; Dunn et al., 1999). Population and assemblage characteristics were determined from unpublished survey data. Based on this information, two species that had high abundances were targeted. *Amblema plicata* (Say, 1817), threeridge, is distributed widely throughout central and eastern North America, ranging from Gulf of Mexico to Mississippi and Atlantic coastal drainages (Williams, Bogan, & Garner, 2008). *Quadrula houstonensis* (Lea, 1859), smooth pimpleback, is endemic to central Texas (Howells, 2002; Howells et al., 1996), and the species is currently listed as 'state-threatened' (TSS, 2010) and a candidate for listing under ESA (USFWS, 2011).

Freshwater mussels generally persist in areas that are stable and protected from scour during higher flows (i.e. hydraulic refugia) (Hardison & Layzer, 2001; Strayer, 1999), and research suggests that relocation is more successful when mussels are transplanted to these refugia (Cope et al., 2003). Therefore, substrate stability was quantified at six candidate sites that had similar species composition within the San Saba River. At each site, bankfull depth and median substrate particle size were determined from six cross-section profiles and surface water slope was determined from a longitudinal profile. These estimates were used to empirically derive reach-scale bankfull shear stress (i.e. the force of water on the stream bottom) (Statzner, Gore, & Resh, 1988):

$$\tau = \rho \times d \times g \times S$$

where τ is shear stress (N m^{-2}) or force of water in Newtons per unit area, ρ is water density at 25°C, d is mean depth (m) at bankfull, g is the gravitational constant, and S is the slope of the energy line (i.e. water surface slope, m). Substrate instability was then quantified by dividing shear stress by median particle size (Gangloff & Feminella, 2007), where low and high index values correspond to high and low bed stability, respectively (Cobb & Flannagan, 1990). The two sites (Sites 1 and 2) with the lowest comparable substrate instability index were chosen for translocation (Figure 1).

2.2 | Experimental design

In July 2012, adult mussels of similar sizes were collected, marked with 12.5-mm passive integrated transponder (PIT) tags (Biomark, Inc., Boise, Idaho) using marine epoxy putty and assigned to either resident or transplant treatment groups randomly, depending on the number of available mussels at each site (Table 1). PIT tags were used to increase recapture rates of mussels for a more precise estimation of survival probability (Kurth, Loftin, Zydlewski, & Rhymer, 2007). Resident treatment groups were used as controls to compare mussel response variables with transplant treatment groups, and transplant treatment groups consisted of mussels translocated either from Site 1 → Site 2 or Site 2 → Site 1 (Table 1). Each treatment group consisted of five replicates of eight individuals per species (40 mussels) and were studied at the sites using randomized, nested block design, whereby each replicate was assigned randomly to 1 m^2 subplots (blocks) within 16 or 25 m^2 plots (following Cope et al., 2003). Densities within plots were kept at 8 mussels m^{-2}, which was twice that of natural densities in the lower San Saba River (4.5 mussels m^{-2}; unpublished data). In preparation for transport, mussels were wrapped individually in a moist paper napkin and placed inside an unsealed plastic bag. Mussels were then placed into ice chests lined with ice, although cardboard was used to prevent mussels from coming into direct contact with ice or meltwater. Mussels were transported by vehicle to each site for a total of 45 min per trip. This method of transport, in contrast to water transport, was used because of its limited adverse effects on mussels over short distances (Chen, Heath, & Neves, 2001; Yusufzai et al., 2010).

TABLE 1 Treatments (resident and transplant), their respective sample sizes (n), and mean (± SD mm) initial shell length (sl) used to study the effects of relocation on survival and growth of freshwater mussels (*Amblema plicata* and *Quadrula houstonensis*) in the San Saba River, Texas

	Amblema plicata		*Quadrula houstonensis*	
Treatment	**n**	**sl**	**n**	**sl**
Site 1				
Resident	40	79.7 ± 13.2	40	59.5 ± 4.4
Transplant	--	--	40	49.5 ± 6.6
Site 2				
Resident	--	--	40	46.8 ± 5.1
Transplant	40	89.4 ± 5.7	--	--

2.3 | Post-translocation monitoring

Survival, growth and body condition were measured every 4–5 months after translocation (seven site visits in total) for 2 years. During each assessment, mussels were collected using an antenna receiver by pinpointing the location of PIT tags, combined with visual and tactile searches within and around the study plots. The entire site was searched to recover dead mussels, or on rare occasions live mussels that became dislodged from the plots, and searching ended once all individuals were recovered or PIT tags were no longer detected with the antenna receiver (1–3 d per site). Mussels were placed into mesh bags submerged in areas with sufficient flow until they were processed. Processing time for each mussel was limited to ≤7 min to minimize stress-related responses from handling and aerial exposure. During that time, encounter history for each mussel (live, dead or not encountered) was documented and shell length (mm) and wetted weight (g) were measured to estimate yearly proportional shell growth (mm yr^{-1}) and Fulton's K body condition factor, respectively:

$$\text{shell growth rate} = \frac{\text{new shell growth/initial shell length}}{\text{time (yr) since the begining of the study}}$$

$$\text{Fulton's K} = \frac{\text{wetted weight}}{\text{shell length}^3} \times 10^6$$

2.4 | Statistical analyses

Prior to translocation, analysis of variance (ANOVA) was used to compare mean instability index among the six potential translocation sites as part of the site selection process. Tukey's honestly significant difference post hoc test was then used to contrast differences in mean instability index between sites. At the completion of the study, mark-recapture and regression techniques were used to model survival probability, shell growth and Fulton's K index. Akaike's Information Criterion (AIC) or quasi-likelihood AIC corrected for small sample sizes ($QAIC_c$) was used to identify the most parsimonious model within each candidate set (Burnham & Anderson, 2003). Top-ranked models were considered to have substantial support when ΔAIC or $QAIC_c < 2$, but models fitting this criterion with a difference of only one parameter and minimal difference in maximum log-likelihood were not considered (Arnold, 2010; Burnham & Anderson, 2003). AIC or $QAIC_c$ weights (w) were also used to assess the relative importance of each model based on ratios between model weights (i.e. evidence ratios) (Burnham & Anderson, 2003).

Survival probability was estimated using a joint live and dead encounter mark–recapture model (Burnham's model) in R package RMark (Laake, 2013) to build models in program MARK (Burnham, 1993; Lebreton, Burnham, Clobert, & Anderson, 1992; White & Burnham, 1999). Burnham's model was used to estimate four parameters: (1) survival probability (S), the probability of surviving to the next encounter interval; (2) recapture probability (p), the probability of being found alive; (3) recovery probability (r), the probability of being found dead; and (4) fidelity (F), the probability of remaining in the study area. Assumptions of this model are as follows: (1) all marked individuals have the same probability of surviving and being recaptured; (2) tags were not lost; (3) dead recovery rates were constant; (4) encounter intervals were relatively short in duration; and (5) dead recoveries occurred outside the sampling area (Burnham, 1993; Lebreton et al., 1992). The main objective here was to estimate survival probability; therefore, recapture and recovery probabilities were considered nuisance parameters, and fidelity was fixed to 1 for all models because dead individuals were recovered within the sampling area only.

Survival probability was estimated using a hierarchical approach by first estimating recapture and recovery probabilities from a candidate set of models. Time (i.e. sampling date) and site (Site 1 vs Site 2) were included as predictor variables for recapture and recovery probabilities because environmental conditions in streams vary over time and space. Models of recapture and recovery probabilities were restricted to time and site because PIT tags are known to improve the detection of mussels significantly (Kurth et al., 2007), which nullified any effects (e.g. behavioural) species identity might have on recapture probabilities (Villella et al., 2004), and because treatment should not have an impact on recapture and recovery probabilities. The best-approximating model for recapture and recovery probabilities was then used to model survival probability for each species. Survival probability was modelled with time, site, treatment (resident vs transplant) and initial shell length as an additive covariate. A bootstrap goodness-of-fit test was used to test for adequate fit, and level of fit was examined by ranking and counting the number of models from 1000 simulations with deviance ≥ observed deviance. Overdispersion was corrected in the analysis by estimating the variance inflation factor ($\hat{c}$ = 1.73), which was calculated by dividing observed $\hat{c}$ by mean estimated $\hat{c}$ from the bootstrap simulations.

Linear mixed models (LMMs) and generalized additive mixed models (GAMMs) were used to examine variation in Fulton's K condition factor and yearly proportional growth rate, respectively. Mixed effects models are useful regression analyses for grouped data because of their flexibility in handling covariance structures and unbalanced designs (Pinheiro & Bates, 2006). The response variables for each species were modelled separately and included time as a continuous fixed variable, site and treatment as fixed categorical grouping variables, and replicate as a random, blocking variable, which was also used to account for non-independence of repeated measures over time (Pinheiro & Bates, 2006). The R package *mgcv* (Wood, 2001) was used to model growth with GAMMs using a Gaussian identity link function and cubic smoothing splines (Zuur, Ieno, Walker, Saveliev, & Smith, 2009; Zuur, Saveliev, & Ieno, 2014). Significances of the smoothing term were examined with an F-ratio test and evaluated the fit by the effective degrees of freedom (edf). LMMs were used to model Fulton's K with *lme4* package in R (Bates, 2010) because these data displayed a linear trend over time.

3 | RESULTS

3.1 | Substrate stability

ANOVA indicated there was a statistically significant difference in mean substrate instability index among sites ($F_{5,\ 30}$ = 3.56, P = 0.012). Sites 1 and 2 had index values of 0.24 and 0.49, respectively, which were the lowest among the six sites examined before translocation in the San Saba River (Figure 2). For these two sites, mean substrate instability index was not statistically different based on a Tukey HSD post hoc test.

3.2 | Recapture and recovery probabilities

Of the 16 candidate models used to estimate both live recapture (p) and dead recovery (r) probabilities, the 1st best-approximating model for recapture probability varied by time and site and recovery probability was constant through time (Table 2). The 2nd best-approximating model ($\Delta QAIC_c$ = 1.45) differed by only one variable in that recovery probability varied by site (Table 2). However, the 1st best-approximating model was 2.1 times more supported than the 2nd best-approximating model; therefore, the 1st best-approximating model was advanced to the

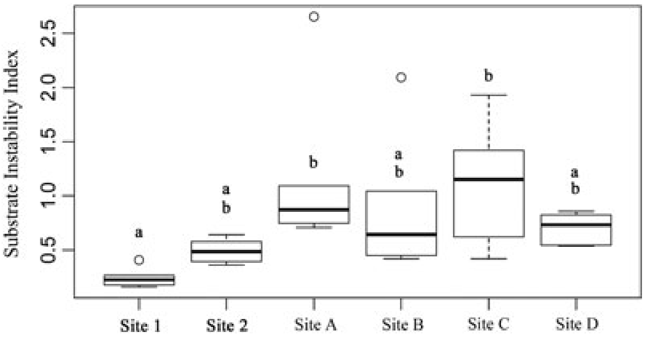

FIGURE 2 Mean substrate instability values among the two relocation sites (sites 1 and 2) and four additional candidate sites (sites A–D). Letters atop each boxplot indicate mean contrasts from Tukey's HSD test, indicating two significantly different groups (a and b). Circles atop boxplots represent outliers

TABLE 2 Top three ranked candidate models of recapture (*p*), recovery (*r*) and survival (*s*) probabilities modelled using analysis of live recaptures and dead recoveries, yearly proportional shell growth modelled using generalized additive mixed models and Fulton's K index modelled using linear mixed models for *Amblema plicata* and *Quadrula houstonensis* in the San Saba River, Texas, USA. Recapture and recovery probabilities were modelled first with the most complex model for survival probability [*s*(time × site × treat + length)], and survival probability was modelled with the top ranked model for recapture and recovery probability [*p*(Time + Site) *r*. F_1]. Dot notation indicates a time-invariant model. Statistics include the number of parameters for a model (*k*), Akaike's Information Criterion (AIC) or quasi-likelihood AIC corrected for small sample sizes (QAICc), change in AIC or QAICc and model weights (w_i)

Parameter/species	Model	k	AIC/QAICc	ΔAIC/QAICc	w_i
Recapture and recovery probabilities					
Both species	*p*(Time + Site) *r*. F_1	12	265.03	0.00	0.37
	p(Time + Site) *r*(Site) F_1	13	266.48	1.45	0.18
	p(Time + Site) *r*(Time) F_1	13	267.06	2.03	0.13
Survival probability					
Amblema plicata	*s*(Treat)	4	43.77	0.00	0.35
	s.	4	44.33	0.56	0.27
	s(Time)	5	45.98	2.21	0.12
Quadrula houstonensis	*s*(Treat)	6	357.99	0.00	0.48
	s(Treat + Time + Length)	8	360.03	2.04	0.17
	s(Site + Time + Length)	8	361.63	3.64	0.08
Yearly proportional shell growth					
Amblema plicata	Time × Treat + Length	-	−329.14	0.00	1.00
	Time × Treat	-	−311.60	17.53	0.00
	Time + Treat + Length	-	−291.78	37.36	0.00
Quadrula houstonensis	Time	-	−440.90	0.00	0.58
	Time + Length + Site	-	−437.73	3.17	0.12
	Time + Length	-	−437.66	3.24	0.12
Fulton's K body condition index					
Amblema plicata	Time × Treat + Length	-	464.49	0.00	0.98
	Time + Treat + Length	-	472.66	8.17	0.02
	Time + Length	-	482.14	17.65	0.00
Quadrula houstonensis	Time + Site + Treat + Length	-	796.71	0.00	0.54
	Time × Site × Treat + Length	-	797.00	0.28	0.49
	Time + Site + Length	-	828.01	31.40	0.00

candidate set used to model survival probability. Recapture probabilities for both sites were high but declined slightly over time, and Site 2 (0.98–1.00) was consistently higher than Site 1 (0.91–0.98) over the 2-year period (Figure 3a). Moreover, the probability of recovering a dead individual was 0.48 at both sites and was constant through time (Table 2).

3.3 | Survival probability

Nine candidate models were considered when modelling survival probability for *A. plicata*, and the 1st best-approximating model for this species varied by treatment (Table 2). The 2nd best-approximating model was also competitive ($\Delta QAIC_c$ = 0.56) but was time invariant (Table 2). However, because the 1st best-approximating model was only 1.3× more supported than the 2nd best-approximating model and the 2nd best-approximating model had fewer parameters, it is more plausible that the 2nd best-approximating model was the most parsimonious (Table 2). Estimates derived from the most parsimonious model indicated that survival probabilities for *A. plicata* were 1.00 and 0.99 for resident and transplant treatments, respectively (Figure 3b). Of the 14 candidate models used to estimate survival probability for *Q. houstonensis* only one model was considered informative ($\Delta QAIC_c < 2.00$). This model indicated that survival probability varied by treatment. Estimates derived from this model indicated that survival probabilities for resident and transplant treatments were 0.97 and 0.85, respectively, indicating significantly lower survival probability for the transplant treatment (Figure 3c).

3.4 | Shell growth

Yearly proportional shell growth for *A. plicata* was modelled in a candidate set of six models. The most parsimonious model (AIC *w* ~ 1.00) among them varied by time, treatment and initial shell length, which included an interaction between time and treatment (Table 2). Parameter estimates for this model (Table 3) and mean shell growth plotted over time (Figure 4a) indicated that shell growth of *A. plicata* in the resident treatment at Site 1 was higher than the transplant treatment from Site 1 → Site 2. Of the nine candidate models considered for *Q. houstonensis*, the 1st best-approximating model (AIC *w* ~ 0.58) showed that shell growth varied only by time (Table 2) and was 4.8× more supported than the next best-approximating model (Table 2). Parameter estimates for this model (Table 3) and mean shell growth plotted over time (Figure 4b) indicated that shell growth of *Q. houstonensis* was similar between resident and transplants and generally declined over time.

3.5 | Fulton's K body condition index

Of the six candidate models considered for *A. plicata*, the 1st best-approximating model (AIC *w* = 0.98) showed that Fulton's K body condition index varied by time, treatment and shell length, which included an interaction between time and treatment, and this model was more than 49× more supported than the next best-approximating model (Table 2). Parameter estimates for the 1st best-approximating model

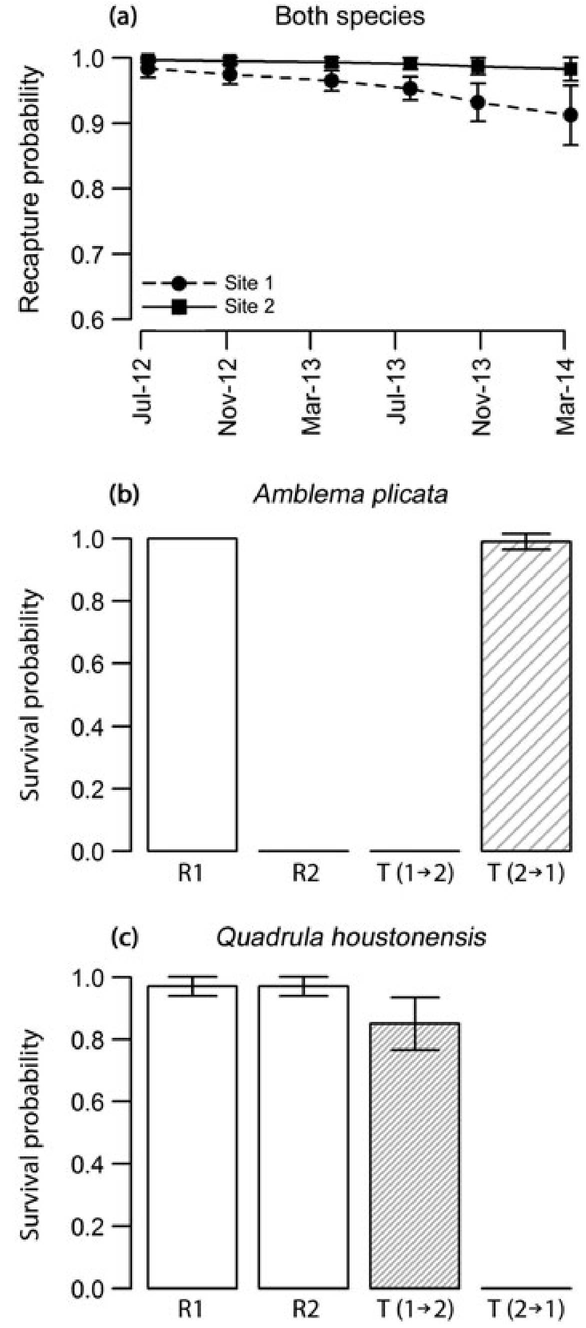

FIGURE 3 Parameter estimates for recapture probability over time for both sites (a) and survival probability for *Amblema plicata* (b) and *Quadrula houstonensis* (c). Barplots represent time invariant survival probability derived from best-approximating models (Table 2).

(Table 3) and mean Fulton's K plotted over time (Figure 4c) indicated that Fulton's K index of *A. plicata* followed a similar pattern observed for shell growth such that Fulton's K was higher for the resident treatment at Site 1 compared with the transplant treatment from Site 1 → 2, although it was initially higher in the first few months following translocation. Fourteen candidate models were considered when modelling Fulton's K condition index for *Q. houstonensis*. The 1st best-approximating model indicated that Fulton's K varied by time, site, treatment and shell length (Table 2). The 2nd best-approximating model was also supported ($\Delta AIC = 0.28$) but only differed from the 1st best-approximating model (1.1× more supported) in that it included an interaction term between time, site and treatment (Table 2). Parameter estimates for the 1st best-approximating model (Table 3) and Fulton's K index plotted over time showed that Fulton's K of *Q. houstonensis* was slightly lower in the resident treatment at Site 1 than either the resident treatment at Site 2 or transplant treatment from Site 2 → 1 (Figure 4d).

4 | DISCUSSION

4.1 | Survival probability

Survival probability of *Amblema plicata* and *Quadrula houstonensis* was minimally affected by translocation in this study. Survival probability of *A. plicata* was greater than 0.99 for both the resident and transplant treatment groups, and although there was a statistically significant difference between the treatments, the size of the effect (0.01) was small and probably not biologically relevant. The high survival probability for this species may be a function of its life history and general tolerance to environmental perturbations. For example, Hart, Grier, Miller, & Davis (2001) found that *A. plicata* populations occurring in the Mississippi River had naturally high survival probabilities (> 0.99). Dunn et al. (1999) found that recovery and survival of *A. plicata* translocated throughout the Mississippi and St. Croix Rivers were 85.8 ± 3.9% (SE) and 89.0 ± 9.1%, respectively. After the second year of monitoring, Dunn et al. (1999) reported similar percentages of recovery (86.7 ± 4.3%) and survival (97.0 ± 1.6%). Survival probability for *Q. houstonensis* also was high (> 0.85) for both resident and transplant treatments, but there was a significant difference between treatments, and unlike *A. plicata*, the size of the effect was larger (0.12), which might indicate that translocation had an adverse effect on this species. Cope et al. (2003) found that *Quadrula pustulosa* (Lea, 1831), pimpleback, a species closely related to *Q. houstonensis* (Serb, Buhay, & Lydeard, 2003), had high survival rates (~80%) 3 years after translocation in the St. Croix River, Minnesota, USA. Studies by Havlik (1997), Dunn et al. (1999), Cope et al. (2003) and Peck et al. (2014) have similarly reported high survival rates for other species of mussel translocated across sites. The results of the present study corroborate previous findings and add to the growing body of literature indicating that translocation, when implemented properly, can have minimal impacts on the survival of mussels. Previous studies, including the present one, however, have primarily focused on adult mussels and little is known about the feasibility of juvenile translocation (Cosgrove & Hastie, 2001), although there is some evidence from captive-bred juveniles (Kyle, Reid, O'Connor, & Roberts, 2017).

4.2 | Shell growth and body condition

Shell growth and body condition of mussels were affected by translocation but only in some treatment groups. For *A. plicata*, shell growth and Fulton's K index were lower in the transplant treatment from Site 1 → Site 2 than the resident treatment at Site 1, suggesting that this species might have experienced reduced growth from translocation. However, treatment effects were not observed for *Q. houstonensis*, but growth was lowest in the resident treatment at Site 2. The consistently lower shell growth at Site 2 for both species could indicate that

TABLE 3 Coefficients for the top generalized additive mixed model (GAMM) for growth and linear mixed model (LMM) for Fulton's K condition index, including fixed effect (estimate, standard deviation and *t* statistic) and random effect (intercept variance and standard deviation) coefficients for each model and smoother terms for GAMMs. Approximated estimates for smoothing terms consist of effective degrees of freedom (edf), *F* statistic, and significance level (*P*)

		Fixed effects			Random effects		Smoother		
Parameter/species/model	**Term**	**Est**	**SE**	***t***	**Int (var)**	**SD**	**edf**	***F***	***P***
Growth									
Amblema plicata:	Intercept	0.244	0.035	7.08					
Time × treat + length	Transplant	−0.024	0.003	−7.14					
	Length	−0.002	0.004	−4.88					
	Replicate				0.009	0.010			
	Time × resident	−0.042	0.005	−8.10			4.8	54.5	< 0.01
	Time × transplant	0.001	0.005	0.25			4.1	5.0	< 0.01
Quadrula houstonensis:	Intercept	0.054	0.004	13.09					
Time	Replicate				0.008	0.018			
	Time	−0.043	0.005	−8.97			3.56	31.4	< 0.01
Fulton's K									
Amblema plicata:	Intercept	370.89	15.37	24.13					
Time × treat + length	Time	0.04	0.00	8.16					
	Transplant	14.42	2.89	5.00					
	Length	−1.63	0.20	−8.31					
	Transplant × time	−0.02	0.01	−3.32					
	Replicate				10.86	3.30			
	Residuals				32.24	5.68			
Quadrula houstonensis:									
Time + Site + treat + length	Intercept	548.17	23.25	23.58					
	Time	0.06	0.00	13.50					
	Site 1	50.38	5.89	8.56					
	Transplant	−28.34	4.46	−6.35					
	Length	−3.24	0.50	−6.55					
	Replicate				26.94	5.19			
	Residual				92.10	9.60			

the treatment effects in models of *A. plicata* growth might be due to differences in habitat quality between sites. For example, in transplanted populations of the Louisiana pearlshell, *Margaritifera hembeli* (Conrad, 1838), Bolden & Brown (2002) found site and habitat-specific effects on shell growth of resident and transplanted mussels. Kesler et al. (2007) demonstrated in a long-term reciprocal transplant study that shell growth varied between translocation sites, which they attributed to differences in food availability. Differences in shell growth between treatments observed in this study also could have been driven, in part, by the differences in size of individuals between treatments, but this relationship was not consistent across all treatments. Thus, habitat quality is likely to have been responsible for differences in *A. plicata* growth, although further study with proper controls is needed. The mismatch between the effects observed on survival probability but not shell growth processes for *Q. houstonensis* is unexpected as stress-induced responses from translocation or resource limitation should presumably influence growth first rather than more important functions such as maintenance and survival (Jokela & Mutikainen, 1995). This pattern further supports the conclusion that the difference in survival probability for *Q. houstonensis* between treatments is small and may not be biologically relevant.

4.3 | Potential factors affecting translocation success

The results of this study demonstrate that site selection is a major contributor to the success of mussel translocation, corroborating previous research on this method (Bolden & Brown, 2002; Cope et al., 2003; Dunn et al., 1999; Peck et al., 2014). For example, Dunn et al. (1999) concluded after conducting several translocations in the north- and south-eastern USA that success was influenced primarily by high habitat suitability, proper handling and transport procedures, and the time of year translocation took place. Cope et al. (2003), who evaluated the recovery and survival of mussels in the St. Croix River, came to the same conclusion that high mussel survival was directly related to proper handling and transport protocols and selection of suitable translocation sites, which they inferred from substrate stability of sites. Protocols for site selection in this study, based on population characteristics and substrate stability, seemed to be important factors for minimizing stress of mussels, and studies should follow a similar quantitative approach to selection of translocation sites (Cope et al., 2003).

Perhaps equally important to the success of mussel translocation are procedures used in the handling of live specimens (Dunn et al., 1999). Collecting and processing mussels during translocation and post-translocation monitoring can affect mussels by exposing them to rapid temperature fluctuations (e.g. from emersion or aerial exposure) and limiting respiration and food intake, which in turn, can hinder metabolic processes (Byrne & McMahon, 1994), reduce shell growth (Haag & Commens-Carson, 2008) and increase mortality rates (Dunn et al., 1999). Limiting handling effects of translocation are thus achievable under certain procedures and environmental conditions (Bartsch, Waller, Cope, & Gutreuter, 2000; Byrne & McMahon, 1994; Cope

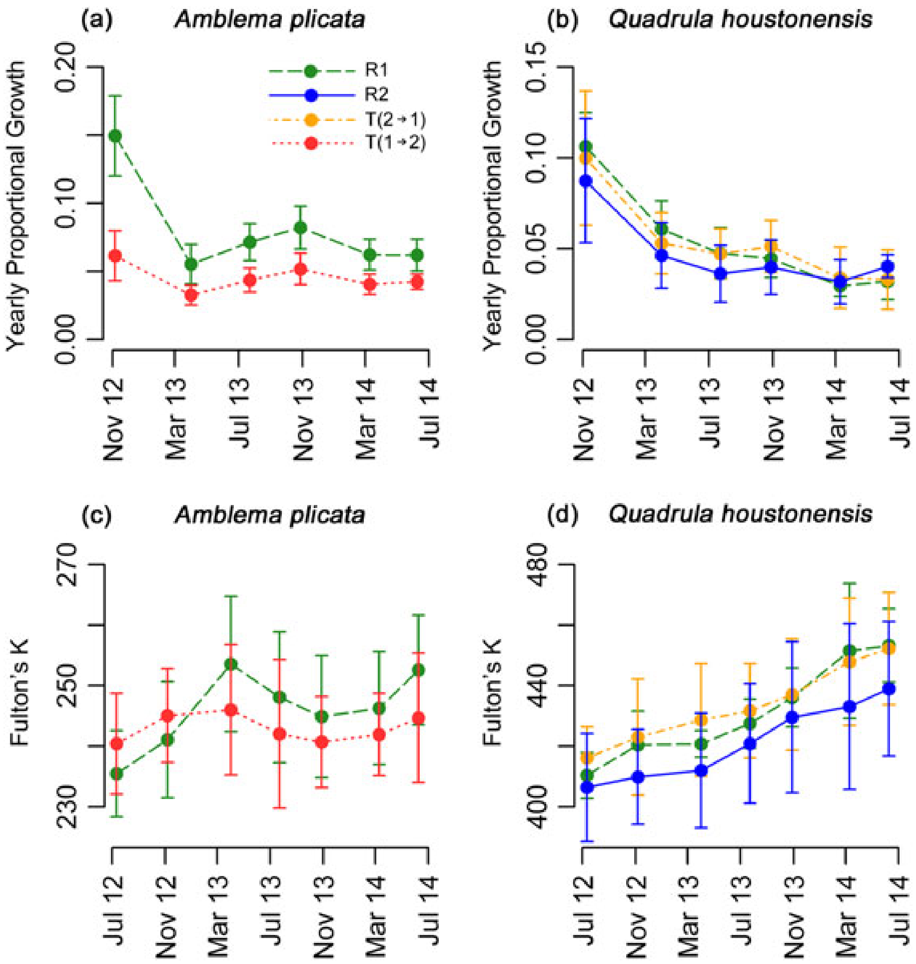

FIGURE 4 Mean yearly proportional growth rate (a and b) and mean Fulton's K body condition index (c and d) for *Amblema plicata* and *Quadrula houstonensis*

et al., 2003; Dunn et al., 1999; Waller et al., 1999). For example, Bartsch et al. (2000) found that when mussels were emersed for <1 hour at temperatures ranging from 15 to 35°C, survival rates were high and burrowing ability was unaffected, and Cope et al. (2003) argued that emersion times of 15–60 min have been shown to have limited influence on mussel survival. Handling effects in the present study were minimized by storing mussels in meshed bags submerged in areas of the stream with adequate flow, and handling and emersion of mussels were limited to ≤7 min during processing. Stress was also minimized during transport of mussels by keeping them moist and cool for the duration of the trip, following recommendations by Dunn et al. (1999) and Chen et al. (2001).

Relocating mussels during certain times of year has been implicated as an important factor affecting mussel survival, mainly because temperature is directly related to metabolic processes of freshwater mussels (Byrne & McMahon, 1994). For example, Dunn et al. (1999) observed higher mortality rates when mussels were translocated in relatively cool months versus mussels relocated during moderate to warm months, and they reasoned that complex substrate coupled with cold water conditions inhibited the ability of the mussels to burrow into the substrate. Indeed, the positive relationship between burrowing performance and water temperature has been demonstrated experimentally (Block, Gerald, & Levine, 2013; Waller et al., 1999). High temperatures can be equally detrimental to physiological processes of mussels if temperatures approach or exceed upper thermal tolerance limits, at which point mussels may experience reduced metabolic activity (Galbraith, Blakeslee, & Lellis, 2012; Ganser, Newton, & Haro, 2015). In addition to temperature, the time of year mussels are translocated can be important since handling can disrupt reproductive activity or cause premature release of glochidia (Lefevre & Curtis, 1910; Yeager & Neves, 1986). Despite these possible effects, the time of year mussels were translocated in this study appeared not to have an impact on survival, even though mussels were translocated in July during abnormally hot and dry conditions. Daily air temperature during the days translocation took place ranged from 21.7–40.6°C and averaged 30.1°C. However, because emersion was limited to ≤7 min, it is likely that mussels were protected from ambient conditions. In addition, the San Saba River is a spring-fed river, and as such, water temperatures were relatively cool, ranging from 26.8–31.1°C and averaging 28.8°C, which was apparently enough to protect mussels from rising water temperatures throughout the region.

4.4 | Implications for conservation

Despite the frequent use of species translocation, it has not received widespread acceptance within the conservation community, in part, because of the lack of experimental evidence demonstrating its success (Fischer & Lindenmayer, 2000). It is therefore important that resource managers and conservation scientists continue to study translocation and other management techniques, particularly among regional faunas because variability in life-history traits (e.g. survival, growth and reproduction) coupled with habitat heterogeneity over landscapes can affect individuals and populations differently (Martone & Micheli, 2012; Bromley, McGonigle, Ashton, & Roberts, 2016). Increasing efforts on improving species translocation will also broaden its applicability to other purposes and give managers the option of translocating populations in response to emerging threats. In particular, climate shifts and corresponding changes to habitat are expected in the foreseeable future, especially as they relate to water resources (Vorosmarty, Green, Salisbury, & Lammers 2000), and native species may be exposed to conditions that exceed their capacity of normal adaptive responses (Weeks et al., 2011); therefore, translocation may be used to establish new populations outside historic ranges (Olden et al., 2011; Weeks et al., 2011).

Freshwater mussels are sensitive to impacts on aquatic ecosystems (Downing et al., 2010; Vaughn & Taylor, 1999), and thus can be used as a model for studying species responses to environmental change and conservation techniques. To date, mussel translocation is used most frequently to avoid stressors from in-stream construction activities (Cope & Waller, 1995; Peck et al., 2014), but impacts sustained to aquatic habitat may require the use of translocation for facilitating gene flow among fragmented populations (Galbraith et al., 2015) or assisting with the establishment and colonization of new populations, which has received little attention by malacologists (Haag & Williams, 2014). However, caution should always be exercised when translocating populations because of the potential adverse consequences, such as mixing distinct evolutionary significant units or increasing disease transmission (Sime, 2015; Villella, King, & Starliper, 1998). Appropriate planning should be implemented on a case-by-case basis when considering translocation (IUCN/SSC, 2013). Moreover, additional research is needed to evaluate long-term effects of mussel translocation, and whether translocation between populations influences population demographics or even meta-population and community dynamics (Haag & Williams, 2014). We predict that translocation will become increasingly used in species management, and our results contribute to the broader knowledge of translocation needed for its successful implementation in future conservation programmes.

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