Received: 17 August 2020 | Revised: 31 May 2021 | Accepted: 26 June 2021

DOI: 10.1111/jbi.14232

Journal of Biogeography WILEY

RESEARCH ARTICLE

Unlocking the history of a trans-Atlantic invader: Did the human slave trade impact Brown mussel dispersal?

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Funding information
U.S. Department of Agriculture; Fundação para a Ciência e a Tecnologia; National Research Foundation of South Africa, Grant/Award Number: 64801; University of Central Florida; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior; Fulbright Association; FCT-MEC, Grant/Award Number: IF/01413/2014/CP1217/CT0004 and UIDB/04326/2020

Handling Editor: Sergio Floeter

Abstract

Aim: Brown mussels exhibit a trans-Atlantic distribution putatively caused by either native dispersal or artificial gene flow, likely in concert with the transport of enslaved people from Africa. Evolutionary history and demographic models of this widespread species may clarify how the present-day distribution was impacted by natural versus artificial dispersal. Particularly, dating the timing of the South American/African split may determine whether the human slave trade likely impacted the contemporary distribution of brown mussels.

Location: Coastal Brazil, Morocco, South Africa, and Mozambique.

Taxon: *Perna perna* (Linnaeus 1758).

Methods: We genotyped a total of 644 samples from 18 populations at 10 microsatellite loci. We estimated genetic structure with clustering algorithms in STRUCTURE and GENETIX. We estimated genetic distances by characterizing patterns of pair-wise F_{ST} using the program FSTAT, evaluating differences among and between regions via AMOVA, and testing isolation by distance in IBDWS. To estimate and date the most likely pathway by which *P. perna* crossed the Atlantic Ocean we used Bayesian factors from thermodynamically heated coalescent simulations in the program MIGRATE-n.

Results: We found no general pattern of reduced or elevated levels of genetic diversity within any region across site or locus. We identified four genetic clusters: East South Africa (ESA), West South Africa (WSA), Brazil (BR) and North Africa (MO); F_{ST} ranged from 0.06 to 0.11 among regions and exhibited a significant pattern of isolation by distance. Migration models indicated that *P. perna* dispersed from WSA to MO and from there to BR of approximately 2,000 years.

Main conclusions: Multiple lines of evidence suggest the Brazilian populations of *P. perna* have been a long-standing native population, originating from northern Africa and are unlikely a consequence of the African slave trade. Although, human introduction cannot be ruled out South American *P. perna* populations exhibited genetic characteristics indicative of a divergent, isolated and established population, featuring the genetic signature expected for a native population.

KEYWORDS
biological invasions, brown mussel, cryptogenic, demographic modelling, human slave trade, microsatellites

1 | INTRODUCTION

The potential harm offered by biological invasions to public health, agriculture and biodiversity is well-established (IMO - International Maritime Organization, 2001). Moreover, damage caused by invasive species highlights the importance of assessing the characteristics of invasion success to better understand what promotes the spread of non-native species and to develop management actions (IMO - International Maritime Organization, 2001). However, inferring processes after a successful invasion is challenging, largely due to a lack of information about the biological invasion history (Estoup & Guillemaud, 2010). It can be difficult to determine the biogeography of invasive species because they are often detected years, decades or even centuries after the introduction event took place (Crooks, 2005; Kowarik, 1995).

The transport of enslaved people from Africa to the Americas is well-known for its social and economic impact and is considered one of the first forms of globalization (Harms, 2002). The slave trade lasted between the 15th and 19th centuries (1501–1888) with an estimate of fifteen to twenty-five millions of enslaved people landing in the Americas during that time (Curtin, 1969; Voyages Database, 2009). Some studies have addressed the impact of this activity on the environment based on economic development such as deforestation, agricultural impacts (e.g. production of wheat, sugar cane, cotton), and the spread of weeds, land animals and their associated diseases (e.g. goats, pigs, chicken, rats and mosquitoes; Baskin, 2002; Crosby, 1986). However, few studies have relayed the impacts of the slave trade to biogeographical patterns of marine species. These few studies include the transport of shipworms and gribbles (wood-boring crustaceans isopod) along with barnacles, seaweeds and sea squirts that hitchhiked on the hulls of wooden ships sailing across the Atlantic (Carlton, 1996).

Mussels and other shellfish are notoriously good invaders, likely because of life history characteristics enabling survival under variable conditions, such as continuous reproduction, fast growth rate, early reproduction, and resistance to environmental change (Karatayev et al., 2007; Ludyanskiy et al., 1993; Rajagopal et al., 2006). When seeking to identify the evolutionary history of invasions, studies of marine invasion genetics have generally found that introduced populations are characterized by high genetic diversity (e.g. *Crepidula onyx*, Woodruff et al., 1986; *Macoma balthica*, Meehan et al., 1989; *Mytilus galloprovincialis*, Grant & Cherry, 1985; *Potamocorbula amurensis*, Duda, 1994; *Mytella charruana*, Calazans et al., 2017; Gillis et al., 2009) as result of high propagule pressure (Rius et al., 2014). Based on genetic similarity between invaded and native populations, a number of studies have been able to use molecular genetic tools to identify sources of origins of invasion (e.g. Astanei et al., 2005; Calazans et al., 2017; Pigneur et al., 2011; Stepien et al., 2002).

The brown mussel *Perna perna* (Linnaeus 1758), is a marine bivalve belonging to the Mytilidae family. This species is a key ecosystem engineer in intertidal to subtidal habitats and is of economic importance as a source of human food (Resgalla Jr. et al., 2008; Siddall, 1980). Along the Atlantic coast of South America *P. perna* has been described as a native species (Venezuela; Southeastern Brazil to Uruguay; Ihering, 1897; Klappenbach, 1965; Rios, 2009; Vakily, 1989). In addition to the Atlantic, *P. perna* naturally occur across a wide-range throughout the old world, including the Red Sea, the Gulf of Aden, east and west coasts of Africa, and in the Mediterranean Sea (Lourenço et al., 2017; Sidall, 1980; Vakily, 1989). *P. perna* was recorded as invasive in the Gulf of Mexico in the early 1990s (Holland, 2001) and was reported in southern Portugal, probably by a range expansion promoted by rising water temperatures (Lourenço et al., 2012). Interestingly, recent studies have suggested that *P. perna* was an anthropogenic introduction to the Brazilian coast based on the lack of *P. perna* shells in ancient shell middens (i.e. sambaquis) from Rio de Janeiro State (dating 2–8 ka). Therefore, the prevailing explanation for the occurrence of *P. perna* in the new world is that *P. perna* were introduced to the Atlantic coast of South America associated with the transatlantic human slave trade, circa 500 years ago (Fernandes et al., 2008; Souza et al., 2003, 2004, 2010; Silva et al., 2018).

The goal of this study is to clarify the new world biogeographical origins of *P. perna*. Specifically, we seek to investigate whether or not *P. perna* is native to the western Atlantic (Brazilian) coast and to estimate the date of arrival to determine if the introduction is associated with the human slave trade. We address these aims by first investigating the overall patterns of genetic diversity and genetic structure of *P. perna* across their range, and second by evaluating demographical models to estimate the migration path and timing of when Brazilian populations diverged from African populations. Using microsatellite markers, we test our predictions that, (1) new world populations would be most closely related to north African populations, (2) new world populations would exhibit reduced genetic diversity compared to old world populations, and (3) the timing of the new world invasion would originate circa 500 years ago. These predictions are grounded in previous studies that have revealed a lack of ancient shell records in the new world (Souza et al., 2003), mtDNA similarity between North African and South American populations (Cunha et al., 2014; Wood et al., 2007), and the possibility of admixture between Africa and South America (Oliveira et al., 2017).

2 | MATERIALS AND METHODS

2.1 | Sampling collection and DNA analysis

A total of 644 samples of the brown mussel, *P. perna*, were obtained from 18 locations: eight in Brazil, three in Morocco, six along the coast of South Africa and one location in Mozambique (Figure 1; Table S1). Mantle tissue (20–30 mg) was dissected from each individual, preserved in 92% ethanol, and stored at −20°C until DNA extraction. Total genomic DNA extraction was performed using a standard proteinase-K protocol adapted from (Sambrook et al., 1989). All individuals were genotyped using a set of 10 microsatellite loci (Coelho et al., 2012) in three multiplex PCR reactions performed in a GeneAmp 9700 thermocycler (PE Applied Biosystems) with volumes of 10 μl containing ±10 ng

of DNA, 0.5 μM of each primer labelled with a florescent marker, 0.2 mM dNTPs (Bioline), 1.5 mM $MgCl_2$, 3.0 μl of 5× PCR Buffer and 0.75 U of GoTaq Polymerase (Promega). Cycling conditions consisted of an initial denaturing step of 5 min at 95°C, followed by 35 cycles of 30 s at 95°C, 30 s at 53 to 59°C as optimization of annealing temperature (Coelho et al., 2012), 40 s at 72°C, and a final elongation step at 72°C for 20 min, with subsequent separation of the PCR products using an ABI PRISM 3130xl DNA analyzer (Applied Biosystems) with Gene Scan Liz 500 as size standard (Applied Biosystems). Microsatellite raw allele sizes were manually scored in STRand 2.4.59 (Toonen & Hughes, 2001). Some of the present samples are the same as used in previous studies: EB (Weber & Silva, 2008); EA, RS, SC, EC, PR, SP (Oliveira et al., 2017); HMP, PLP, PAP, PEP, BAP, PDOP, ES, IM, ML (Cunha et al., 2014).

2.2 | Data analysis

Frequency of microsatellite scoring errors, evidence of large allelic dropout and null alleles at high frequencies were estimated based on the algorithm presented in Brookfield (1996) using the program MICRO-CHECKER (Van Oosterhout et al., 2004). Hardy–Weinberg equilibrium (HWE) was estimated per population and locus with FSTAT (Goudet, 1995). Multiple contrasts of HWE probabilities were corrected according to the sequential Bonferroni procedure (Rice, 1989; Table S2).

We estimated genetic structure with a Bayesian clustering algorithm in STRUCTURE 2.2 (Prichard et al., 2000). We ran the initial analysis assuming that all sampled sites were independent populations capable of forming their own clusters (K = 1 to K = 18). The STRUCTURE analysis was set up with 20 replicate runs performed under the admixture and the correlated allele frequency model with 50,000 Markov Chain Monte Carlo (MCMC) iterations after 500,000 burn-in generations. After the initial number of clusters was defined by the first analysis, we re-ran STRUCTURE for each initially described cluster to determine whether sub-structuring was present. Overall, we identified the best supported number of clusters via Evanno delta K on these successive analyses. Moreover, for a better visual group representation (i.e. across three dimensions) and to uncover population admixture in the absence of model assumptions, such as HWE, we visualized population clustering in a factorial correspondence analysis (FCA) in GENETIX v. 4.05 (Belkhir et al., 2004).

To evaluate genetic differentiation between the Brazilian region and African regions, we estimated genetic distances by characterizing patterns of pair-wise F_{ST} using the program FSTAT (Goudet, 1995). Furthermore, we evaluated differences among and between regions via AMOVA in Arlequin (Excoffier & Heidi, 2010). Also, we tested for

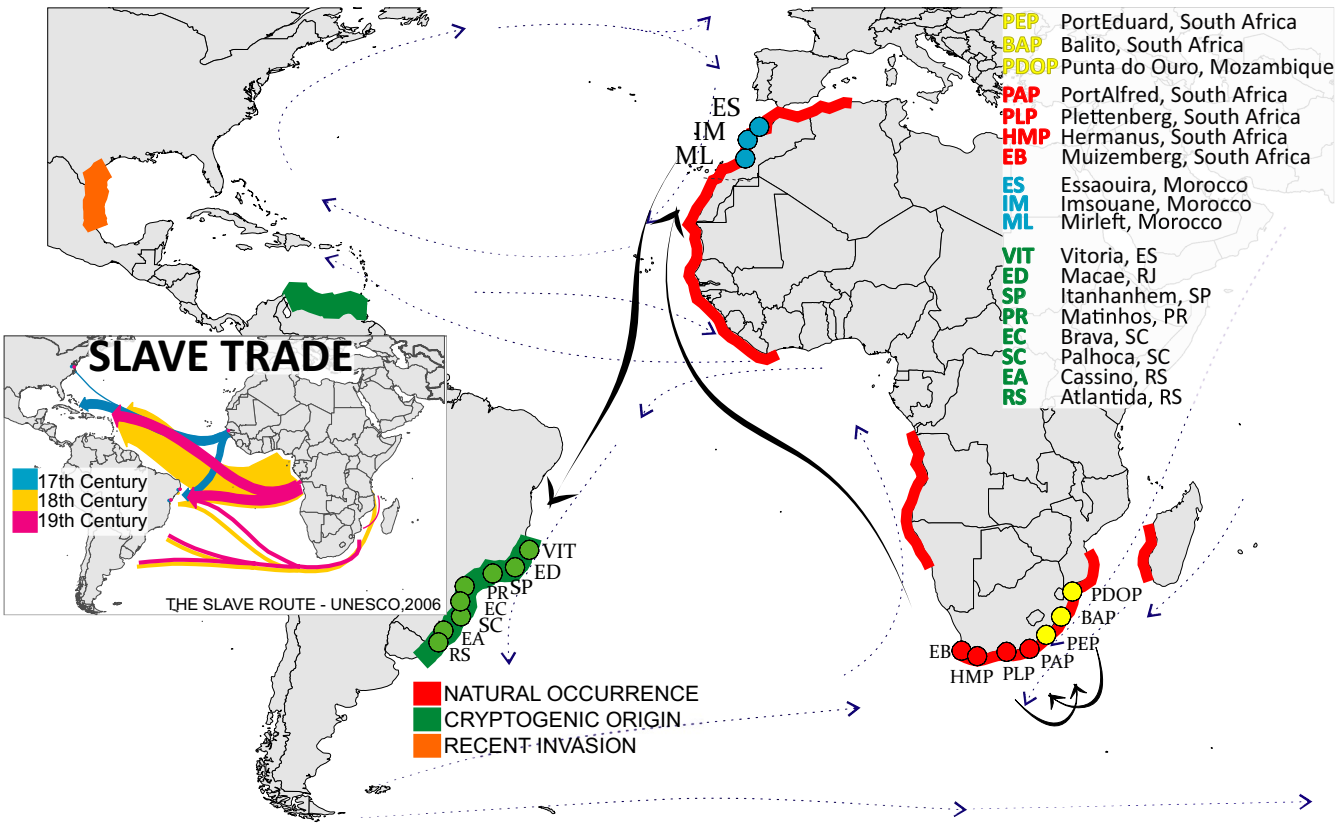

FIGURE 1 Comparing sea currents and routes associated with the slave trade show parallel patterns with regard to the contemporary distribution of brown mussels. The distribution in red shows the natural occurrence, in green the cryptogenic origin, and in orange regions of recent invasion. Sample locations and names of brown mussel populations used in this study are denoted by circles. The bold arrows indicate the most likely migration route of brown mussels. The dotted lines with arrows show the predominant direction of the sea currents

isolation by distance, determining whether *P. perna* populations exhibit a pattern of natural genetic relatedness decaying with geographic distance. Here, we used genetic distance (F_{ST}; Weir & Cockerham, 1984) in a pair-wise analysis with the least-cost geographic distance (shortest over-water distance) between sampling locations (km) estimated in Google Earth Tools 7.1.5.1557 (Google, n.d). Significance was evaluated in IBDWS (Jensen et al., 2005) using a Mantel test with 10,000 randomizations of linearized F_{ST} (i.e. $F_{ST}/(1 - F_{ST})$).

To determine whether patterns of genetic diversity in the new world region were similar to those of the northern or southern African regions, we estimated per population allele frequencies, observed heterozygosity (H_O), expected heterozygosity (H_E) and Allelic Richness (*AR*) using FSTAT (Goudet, 1995). We used a two-way Analysis of Variance (ANOVA) with post-hoc Tukey test in R statistical package version 3.2.3 (R Core Team, 2014) to test whether there were any significant differences among loci and between regions for levels of genetic diversity. Additionally, we compared the mean frequencies of private alleles calculated in GenAlex v.6 (Peakall & Smouse, 2006) among all localities grouped by region, which can be indicative of population isolation in case of presence of uniqueness or may suggest possible recent gene flow by the lack of private alleles between populations.

To estimate the most likely pathway used by *P. perna* to cross the Atlantic Ocean, we used marginal likelihood comparisons (Bayesian factors) from thermodynamically heated coalescent simulations to test how likely the data fit 14 demographic models (Figure 2). We chose our models based on a combination of previous data and possible migration paths proposed for *P. perna* in previous studies (e.g. Wood et al., 2007). Because previous studies found South African populations split into two regions (i.e. East and West; Cunha et al., 2014 and this study, see Section 3), we first tested models differentiating an ancestral East South Africa (Model 1) versus an Ancestral West South Africa (Model 2). Next, we compared simplistic models differentiating an old world origin (Model 3) versus a new world origin (Model 4). The remaining nine models posit more complicated evolutionary histories for *P. perna*. Models 5–7 included different scenarios originating in the old world and spreading to the new world, Models 8–10 include different scenarios with a general South African Origin, Models 11–13 mimic Models 8–10, but do not include the east South African populations (i.e. they are part of a separate lineage), and finally Model 14 posits an ancient unsampled population ('ghost' population) which would be ancestral to Africa, Morocco and Brazil (suggested by P. Beerli, pers. comm.; Figure 2). Tests of our models were conducted in the program MIGRATE-n v. 4.6 (Beerli, 2006), following the methods of Beerli and Palczewski (2010). Our whole data set was used for analysis using the stepwise mutation model for microsatellite DNA loci. We used the default parameters in MIGRATE-n, which estimate all population sizes (θ) and all immigration rates (M) independently by adjusting the interactions among populations by matrix definition. The starting point for genealogy parameters was set using Theta and M values generated from an F_{ST} calculation and with variable constant for all loci. For the Bayesian Markov chain MCMC Strategy settings, we used one long chain with the first 1000 steps discarded as burn-in and the remaining 9000 steps recorded, with an increment of 100 steps, and with the assumption of an equal (and universal) mutation rate among loci. Next, we ranked the marginal likelihoods first for Models 1 versus 2 and then for Models 3–14 to identifying which model best represents the migration path used by *P. perna* populations sampled in this study (Beerli & Palczewski, 2010).

After the coalescent model simulations identified which model best fit our data, we sought to determine the time of the most recent common ancestor for each lineage. Here, we estimated the number of generations since coalescence of populations (represented by posterior distributions) divided by the expected mutation rate (time in generations = divergence (posterior distribution)/mutation rate) for each lineage in the model. The mutation rate used was 10^{-4}, as has previously been described as the best estimate for microsatellites (Inoue et al., 2014; Sun et al., 2012; Whittaker et al., 2003) which is orders of magnitude greater than typical nucleotide substitution rates of 10^{-8}, due to replication slippage of microsatellite loci (Sun et al., 2012). To convert generations to years before present, we used two different estimates for generation time: one year, as suggested by other studies (Cunha et al., 2014; Oliveira et al., 2017) and six months, a more conservative estimate given that *P. perna* typically spawn twice a year and are reproductively active as early as three months (Lunetta, 1969; Mesquita et al., 2001).

3 | RESULTS

All microsatellite loci were highly polymorphic among the 18 populations. The 644 individuals returned 448 alleles, with an average of 45 alleles per locus, ranging from 5 (P02-IM30 and ML30) to 57 (P20-PEP48). However, populations exhibited some loci with a deficit of heterozygotes relative to Hardy–Weinberg proportions (Table S2). This pattern is unsurprising given that other studies have already described this pattern in mollusks in general, and especially in *P. perna* (Coelho et al., 2012; Zardi et al., 2015). Following the methods in Zardi et al. (2015), we used null allele frequency as the basis of locus inclusion in downstream analyses. Tests for null alleles revealed that two loci (P11 and P16; Figure S1) exhibited frequencies above 0.2, the threshold at which loci are characterized by a high frequency of null alleles (Selkoe & Toonen, 2006), and were removed from downstream analyses (Chapuis & Estoup, 2007). The remaining eight loci were included in all downstream analyses.

The STRUCTURE analysis revealed four clusters ($k = 4$) for the three regions studied using the most likely posterior probabilities with the Evanno et al. (2005) criteria. These clusters included the three general regions (South America, North Africa and South Africa), with South Africa further split into eastern and western clusters (Figure 3; Figure S2). The FCA corroborated the structure results, revealing four visual population clusters with the three axes describing 50.3% of the total among-population variation (Figure 4). In light of these results, downstream regional analysis includes the following notation: South America—BR; North Africa—MO; east South Africa—ESA; west South Africa—WSA.

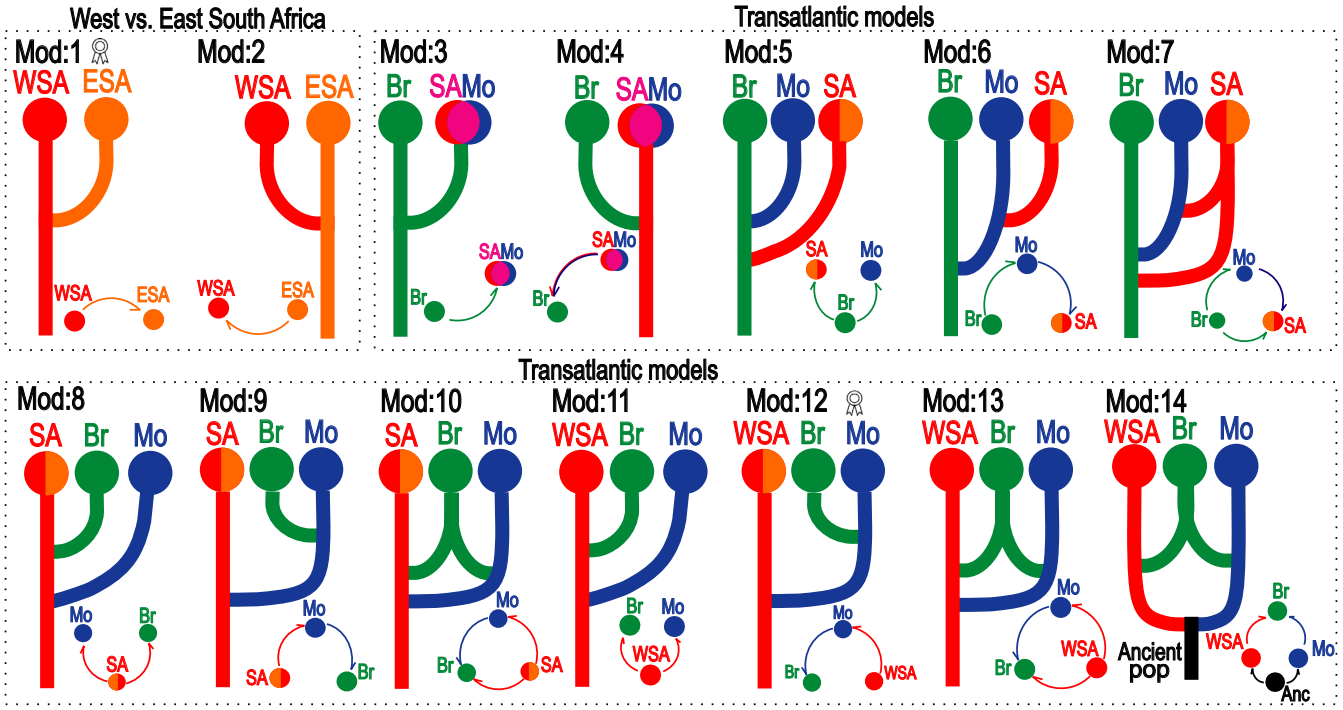

FIGURE 2 Coalescent representations of the models tested to evaluate possible patterns of lineage diversification and population connectivity in *Perna perna*. First, WSA was ancestral to ESA. Second, Africa was the most likely source sending migrants to the New World. The most likely migration pattern (see Section 3) was that *P. perna* dispersed from West South Africa to Morocco, and finally from Morocco to Brazil (Model 12). The ribbon designates the best model for each type of comparison (see Table 1)

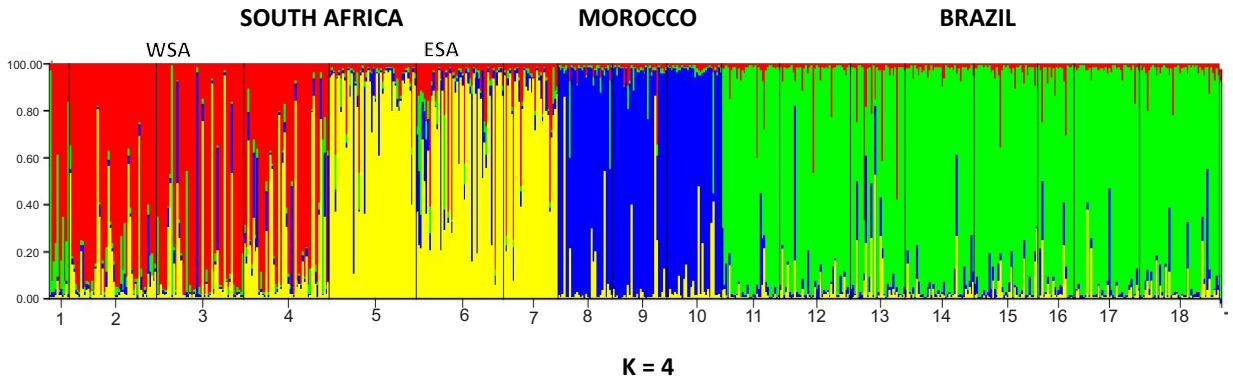

FIGURE 3 Results of Bayesian population genetic structure for microsatellite data indicating four different groups of parent populations ($K = 4$) of *Perna perna*, shown in Red (West South Africa), yellow (East South Africa), in blue (Morocco) and in Green (Brazil). Individual probabilities of assignment are shown on the *y*-axis and are grouped by parent populations calculated by the admixture program in STRUCTURE 2.2

Genetic differentiation (i.e. F_{ST}) between populations (Table S3) and regions indicated genetic isolation among regions ($p < 0.001$). We found that pairwise regional comparisons exhibited similar genetic differentiation (BR-MO, average $F_{ST} = 0.08$; BR-WSA, average $F_{ST} = 0.086$; BR-ESA, average $F_{ST} = 0.10$; MO-WSA, average $F_{ST} = 0.11$; and MO-ESA, average $F_{ST} = 0.09$; Figure S3). The smallest difference was found between the South Africa regions, WSA and ESA, exhibiting an average $F_{ST} = 0.06$ (Figure S3). Genetic and geographical distances exhibited a significant pattern of isolation by distance among all populations (Mantel $R = 0.8066$, $p < 0.001$; Figure S4). However, these results should be taken with caution due to the high variance in distance among populations (see Diniz-Filho et al., 2013).

Overall, population genetic diversity was high within all populations. Allelic Richness (*AR*) and Expected Heterozygosity (H_E) varied between 2.38–12.96 and 0.20–0.99 respectively and the highest allelic richness was recorded at MC_PuntaOuro (12.96) and MR_Mirleft (12.96; Table S4). The analysis of molecular variance (AMOVA) showed that the majority of the variation explained was within populations (94.6%), with variation among regions explaining only 4.69% of the variation (Table S5). Among region differences in

genetic diversity revealed a significant effect of both site and locus as well as a significant interaction effect of site-by-locus for both measures (ANOVA: Site $p < 0.001$, Locus $p < 0.001$, and interaction effect, $p < 0.001$, Figure S5). Given the significant site effect, we ran post hoc tests to determine whether regions differed in genetic diversity. Our analysis indicated that BR and MO were not differentiated in genetic diversity (i.e. *AR* and H_E) but both exhibited significantly less diversity than ESA and WSA (post hoc Tukey test, *AR*: $p < 0.001$; H_E: $p < 0.001$; Table S6). Comparisons between South African regions (ESA and WSA) exhibited a significant interaction between site and locus. The analysis of private allelic genotypes reveal that the BR cluster exhibited the lowest frequency of private alleles (ESA = 0.7; WSA = 1.7; MO = 0.5 and BR = 0.3; Figure S6) indicating that it is likely to be the youngest or less adapted population.

Testing the likelihood of different models of migration, allowed us to reconstruct a best migration model used by *P. perna* populations in the geographical scale studied. First, WSA was ancestral to ESA (Figure 2; Table 1a). Second, Africa was more likely the source of migrants to the New World, than vice versa. When comparing more complex models, the most likely route of migration was that *P. perna* dispersed from WSA to MO, and finally from MO to BR (Figure 2; Table 1b; Model 12). When estimating the time of migration between regions, model estimation showed BR descended from MO before 500 years, with the mode value of the maximum likelihood estimate at 0.4333/μ, with μ = average microsatellite mutation rate (Table S7). The 2.5%–97.5% range of posterior probabilities was 0.000–2.7333. This translates to 2,167 (0–5800) years ago, with our conservative estimate of two generations per year (Table S8). Although the confidence intervals associated with time overlap with zero, and hence cannot rule out human introduction, the mode estimate of time predates the human slave trade.

4 | DISCUSSION

We found that new world populations of *P. perna* were likely founded via a natural geographical expansion from northern Africa approximately 2,000 years ago and not as a consequence of the human slave trade. We identified significant population structure with four primary genetic clusters of *P. perna*. When we compared different demographic models based on a combination of previous data and possible migration paths, we found support for an old world (i.e. South African) origin of *P. perna*. Subsequently, *P. perna* naturally migrated to northern Africa and then crossed the Atlantic to the new world, as represented by our model 12 (Figure 2). Overall, South American *P. perna* populations are closely related to North African populations and exhibit genetic characteristics indicative of a divergent, isolated and established population. In addition, these populations feature the genetic signature expected for a native population with a genetic divergence from Africa having occurred over 500 years ago.

The widespread distribution of *P. perna* falls into four previously described Atlantic provinces: North East Atlantic (NEA); Tropical East Atlantic (TEA); Southwest Indian Ocean and Southwest Atlantic (Floeter et al., 2008). Although there are high levels of endemism within each of these biogeographical provinces, Floeter et al. (2008) conducted genus and species level cluster analyses of reef-fishes and found consistent cross-provincial patterns of connectivity. Processes driving the trans-Atlantic connectivity between Africa and South America are likely influenced by pelagic larval dispersal associated with both the Northern Equatorial Current and the Southern Equatorial Current (e.g. see study by Freitas et al., 2014 and references therein). Indeed, our data suggest that it is likely these currents brought *P. perna* to South America. Within South Africa we found that *P. perna* were split along an east-west gradient. Oceanographic features, together with local adaptation, have been identified as key determinants for the maintenance of phylogeographic breaks along this specific region (Teske et al., 2013). The primary oceanographical influence on the east and south coasts of South Africa is the Agulhas Current. This strong, warm current flows to the southwest along the eastern seaboard of South Africa following the narrow continental shelf (Lutjeharms, 2006). It usually lies 10 km offshore, but it can occasionally flow nearer to the shore at 0 to 1 km offshore (Goschen & Schumann, 1990). Numerous

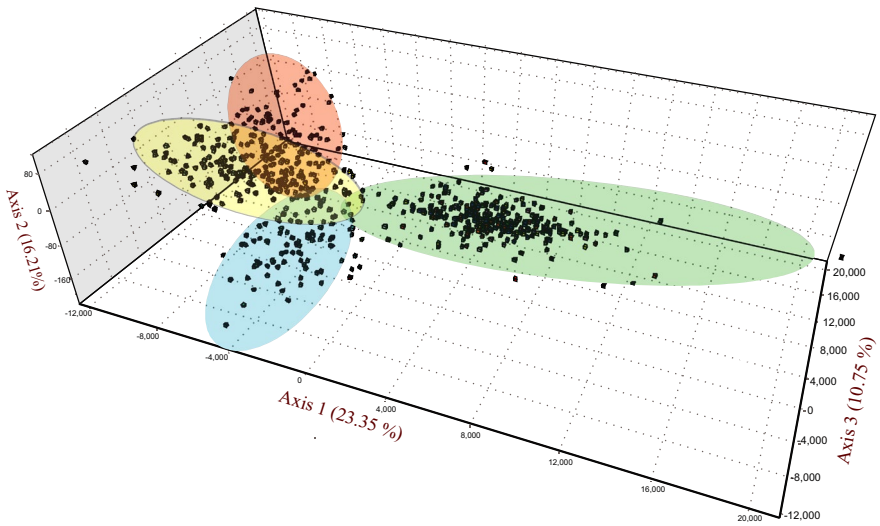

FIGURE 4 Scatter plots of factorial correspondence analysis (FCA) of the microsatellite data indicating regional genetic diversification in *Perna perna*. Each dot corresponds of one individual. The margins of the graphs represent the position of each gravity centre. Each of the four clusters observed here represent the same four different cluster identified by STRUCTURE: red (West South Africa), yellow (East South Africa), blue (Morocco) and green (Brazil)

direct observations indicate that water currents significantly affect the dispersal of the early life stages of fishes and invertebrates (Beckley, 1995; Groeneveld & Branch, 2002). Although, there are examples of dispersal in the direction opposite to the Agulhas Current, mainly by actively dispersing species such as rock lobsters (Groeneveld & Branch, 2002), sardines (Roberts et al., 2010) and dolphins (Mendez et al., 2011), it appears that the passive dispersal of *P. perna* is unable to overcome the current, creating the genetic structure observed between our ESA and WSA populations.

With regard the connectivity of transatlantic populations, our genetic models identified Brazilian populations as likely originating from the same region in Africa where most of Brazilian enslaved people originated (Bight of Benin and Central-West Africa; Voyages Database, 2009), making a good argument for linking South American *P. perna* to the transport of enslaved people. However, if *P. perna* did not get to Brazil via slave trade, then how did they get to Brazil? There are two other possible mechanisms that *P. perna* could have used to cross the Atlantic Ocean approximately 2,000 years ago. First, natural dispersal is possible given that other species show distributions spanning oceans (UNEP-WCMC, 2018). Additionally, natural ocean crossings have been documented with aid of extreme natural events, like hurricanes (Carlton et al., 2017; Houle, 1998). There are many examples of organism that exhibit a post-Gondwana dispersal pattern across the South Atlantic, including plants, freshwater fishes, birds, reptiles and mammals (Briggs, 2003; Censky et al., 1998; Givnish & Renner, 2004; Oliveira et al., 2009). It is likely that *P. perna* migration may have followed a similar system of dispersal. Second, human-aided pre-Columbian Atlantic crossing could also explain the genetic patterns observed here. Similar to *P. perna*, *Mya arenaria* was first documented in sixteenth century Europe after Columbus' voyage, but archeological samples found shells predating Columbus by hundreds of years (Petersen et al., 1992). A possible explanation for the transport of these clams was that Vikings might have carried them back home via incidental transport or as live food (Essink et al., 2017). The same possibility may be held by ocean-going voyagers, crossing the South Atlantic before Columbus's voyage. There is evidence of the possibility that cross-Atlantic rafting can occur in as <100 days (Barragán, 2019; Klink, 1985), however, to date no such evidence of human pre-Columbian South American crossings exists (Moreno-Mayar et al., 2018; Taube, 2004).

Our results match those of C^{14} dated *P. perna* from archaeological sites in Brazil, which suggests shells pre-dated the slave trade (Pierri et al., 2016). Why had other studies found conflicting results? Likely because they did not use as large a sample set as our study. Our study benefited from a collaborative effort which used samples combined from multiple previous studies (i.e. Cunha et al., 2014; Oliveira et al., 2017; Weber & Silva, 2008; Zardi et al., 2015). Although some of these studies independently found results that conflict with this study (Oliveira et al., 2017; Weber & Silva, 2008), our study shows that the accuracy of estimating evolutionary history can be significantly improved by the addition of more taxa and by increasing the spatial coverage of sampling.

If *P. perna* did arrive to the Atlantic coast of South America via the human slave trade, we would expect to see either reduced genetic diversity (owing to a genetic bottleneck) or high genetic diversity (owing to high propagule pressure and/or admixture; Roman & Darling, 2007). Regardless, the genetic pattern ought to match back to a source region, identifying the origin of the invasion (e.g. Stepien et al., 1999). Moreover, we would expect to see reduced private alleles, genetic clustering with one or more 'native' populations, F_{ST} reduced between South America and some 'native' populations, and models showing South America was founded <500 years ago. In this study, we found that South American populations do not exhibit the genetic signatures associated with an invasion (e.g. neither reduced or elevated genetic diversity, nor genetic similarity to a specific native source population) and colonization likely occurred >500 years ago. Indeed, the supporting qualitative evidence (e.g. patterns of genetic clustering, and regional estimates of differentiation) provides further evidence for a natural colonization that pre-dates the Atlantic slave trade.

If *P. perna* is indeed a recent invader (<500 years), it would necessitate at least one of the following three parameters of our demographical models were wrong: (1) Our model posits a microsatellite mutation rate that ranges from 10^{-6} to 10^{-2}, as is the typical range of mutation rates estimated for microsatellites (Table S7; Schlötterer, 2000). But for *P. perna* to have arrived in the past 500 years, the mutation rate would need to be at the extreme high end of these values (e.g. $=/>2 \times 10^{-3}$). Middle and lower microsatellite mutation rates (e.g. $<3 \times 10^{-3}$, Whittaker et al., 2003) generate levels of genetic differentiation too little to be associated with the human slave trade. (2) Selection acting on the mussels, such as a selective sweep among new world populations, would need to drive patterns of diversity to differentiate new world populations relative to old world populations. (3) An unusually fast generation time (<6 months) despite other studies suggesting 1-year generation time for *P. perna* (Oliveira et al., 2017). However, if mutation rates are $=/>2 \times 10^{-3}$ and generation times are <6 months, this would enable the generation of the distinct genetic characteristics necessary to put the time of invasion in line with the human slave trade as a possible vector (Table S8). Moreover, the lower 95% confidence interval associated with our dating of the split between MO and BR includes zero, further providing the possibility of a recent invasion. Although it is possible that *P. perna* is a recent invader, the combined evidence indicates it was likely naturally founded in South America >500 years ago.

Defining *P. perna* as invasive to the western Atlantic coast of South America has numerous political implications. Studies have highlighted the importance of *P. perna* as a natural environmental engineer and as a major source of protein for human consumption (Antunes & Mesquita, 2018; Freitas & Velastin, 2010). However, in Brazil, the Ministry of Environment produced a report listing *P. perna* as an established exotic species (Lopes et al., 2009). Following the status update, the state of Paraná produced a decree to regulate and control production of invasive species (including *P. perna*; IAP - Instituto Ambiental do Paraná, 2009, 2015). Once *P. perna* was categorized as a possible bioinvader in Brazil, Venezuela acted to list *P. perna* as a cryptogenic exotic species (Pérez et al., 2007). Furthermore, studies have discussed strategies for species control (Oliveira, & Machado, 2009; de Souza et al., 2009), following international guidelines for

TABLE 1 All models of migration tested for *Perna perna* with the comparison of maximum likelihood and log-probability of the data (marginal likelihood) as calculated in MIGRATE-n. Models are ranked from least likely to most likely

Model	Description	Log(ml)	LBF	Selected
(a) Models testing South Africa regional relationship				
1: EtoW	East South Africa send to West South Africa	−274050.23	−2077.28	0
2: WtoE	West South Africa send to East South Africa	−271972.95	0	1
(b) Models testing how new world *P. perna* relate to old world *P. perna*				
3: BrtoAf	-Brazil send to Africa	−1011548.81	−739575.86	0
4: AftoBr	-Africa (W&E South Africa and Morocco as on pop) send to Brazil	−1008871.03	−736898.08	0
5: BrtoSa_BrtoMo:	-Brazil send to South Africa and Brazil send to Morocco	−792796.49	−520823.54	0
7: BrtoSa_BrtoMotoSa	-Brazil send to South Africa and Morocco, also Morocco to South Africa	−791133.73	−519160.78	0
6: BrtoMotoSa:	-Brazil send to Morocco that send to South Africa	−790401.71	−518428.76	0
8: SatoBr_SatoMo	-South Africa (W&E) send to Brazil and send to Morocco	−789173.22	−517200.27	0
9: SatoMotoBr	-South Africa (W&E) send to Morocco and after send to Brazil	−785189.12	−513216.17	0
10: SatoBr_Motobr	-South Africa (W&E) send do Brazil also Morocco send to Brazil	−785093.29	−513120.34	0
13: WtoBM_MtoB	-West South Africa send to Brazil and to Morocco also Morocco send to Brazil	−476234.46	−204261.51	0
11: WtoB_WtoM	-West South Africa send to Brazil and also to Morocco	−474354.10	−202381.15	0
14: WtoB_MtoB	-West South Africa send to Brazil and Morocco send to -Brazil (with an previous ancient population preceding South Africa and Morocco)	−474151.10	−202178.15	0
12: WtoMtoB	-West South Africa send to Morocco and after to Brazil	−472712.13	−200739.18	1

Abbrreviations: Log(mL), Bezier approximation score; LBF, Log-Probability of the data given the model (marginal likelihood).

management and control of invasive species (CBD, 2002). In light of the results found in this study, countries in South American may re-evaluate regulations seeking to control or classifying *P. perna* as invasive along the coast especially since the Brazilian population of *P. perna* has already started to present characteristics of a genetic operational taxonomic unit (OTU). Although our results suggest that Brazilian *P. perna* exhibit a genetic pattern of a naturally dispersed population having been founded approximately 2,000 years, it cannot be ruled out that Brazilian *P. perna* populations were introduced by humans. Our results conclude that genetic patterns of isolation observed here would not likely develop naturally in 500 years or less since settlement. Hence, Brazilian *P. perna* populations were unlikely a consequence of the African slave trade.

ACKNOWLEDGEMENTS

The authors are thankful to Brazilian CAPES – National Council for Scientific and Technological Development for the Ph.D. fellowship support to SHCC, and the Brazilian grant program "Science without Borders" and the US Fulbright program for enabling this collaboration. Sample collection was carried out under the following license: No. 37119-3 from the Brazilian Chico Mendes Institute for Conservation and Biodiversity - ICMBIO. This research was also supported by USDA NIFA Award No. 2008-32320-04574 and the University of Central Florida. This research was also funded by Foundation for Science and Technology (FCT-MEC, Portugal [grant numbers: IF/01413/2014/CP1217/CT0004 and UIDB/04326/2020]) and further supported by the National Research Foundation of South Africa (grant number: 64801).

CONFLICT OF INTEREST

The authors have no conflict of interest regarding this publication. And will proceed further in to the process of publication.

DATA AVAILABILITY STATEMENT

Microsatellite data at dryad, accession number: https://doi.org/10.5061/dryad.31zcrjdkx

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BIOSKETCH

This manuscript is part of the PhD project for SC, whose interests involve genetics of invasive species. This research team ties together multiple research groups from Europe, South America and North America to understand the origins of *P. perna* in the new world.

Author contributions: SC, FF, CF and EH conceived the ideas; SC, CL, KN, CT, GZ, FF and ES collected the samples; GZ and KN collected the data; SC and EH analysed the data; and SC, GZ and EH led the writing.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Calazans, S. H., Lourenço, C. R., Nicastro, K. R., Tagliaro, C. H., Zardi, G. I., Ferreira, C. E. L., da C. Fernandes, F., Silva, E. P., & Hoffman, E. A. (2021). Unlocking the history of a trans-Atlantic invader: Did the human slave trade impact Brown mussel dispersal? *Journal of Biogeography*, 48, 2671–2681. https://doi.org/10.1111/jbi.14232