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Research Article

Genetic diversity of divergent redclaw crayfish *Cherax quadricarinatus* (Von Martens, 1868) populations evaluated to initiate a breeding program in Mexico

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ABSTRACT. *Cherax quadricarinatus* is a decapod crustacean of interest to the aquaculture industry. In Mexico, a significant effort has been made to improve biological requirements, but the genetic characteristics are unknown. We examined the genetic diversity and differentiation in four populations in Mexico (three commercial farms and one feral population), as well as one research line from Argentina, used as reference. To initiate a founder stock in a genetic improvement program, we analyzed five microsatellite markers. The genetic diversity in terms of the number of alleles was low to moderate (2.8-6.2) in Mexican populations than the Argentinean sample (8.8). A pairwise Wright's Fst analysis showed that all populations were significantly different ($P < 0.5$). Cross-breeding organisms from a different population are suggested to increase genetic variability before initiating a founder stock with higher genetic variation.

Keywords: *Cherax quadricarinatus*; genetic diversity; microsatellite; breeding program; aquaculture

INTRODUCTION

The redclaw crayfish *Cherax quadricarinatus* is a decapod crustacean of interest to the aquaculture industry for its biological characteristics (Medley et al. 1994, Jones et al. 2000). It was first introduced into Mexico in 1985 by private interests, with failed results. Later, the Federal Government introduced the species in 1995 to evaluate commercial culture's potential (Alvarez et al. 2014). Ponce-Palafox et al. (1999) mentioned that several producers received import permits, with Acuacultivos Santo Domingo in Soto La Marina, Tamaulipas, establishing one of the main stocks in 1998 (Villarreal & Pelaez 1999). The origin of most commercial lines in Mexico can be traced back to a population from Freshwater Australian Crayfish Traders in Tarome, Queensland, Australia. The farm-sourced wild broodstock from the Gilbert and Flinders Rivers in 1984 began testing the species' culture viability (Humberto Villarreal, *pers. comm.*). Up to 10,000 juveniles from this domesticated stock were shipped to the Tamaulipas farm in 1998 and 1999. Over the next few years, Acuacultivos Santo Domingo distributed juveniles and broodstock to several sites in Mexico, including the Northwest Biological Research Center (CIBNOR, acronym in Spanish) in La Paz, Baja California Sur, El Vergel farm in Soto La Marina, Tamaulipas, and La Alberca, a semi-intensive farm near Nueva Italia, Michoacán, geographically isolated from each other (Hernández-Gurrola et al. 2020). El Vergel farm additionally received an undetermined number of offspring from Auburn University in 2005-2008 to conduct research (Nabor Medina-El Vergel farm owner-, *pers. comm.*).

The actual number of commercial farms and production figures in Mexico is difficult to establish. Data for the species is combined with that of other freshwater crustaceans, such as freshwater prawns. However, FAO (2011) reported 50 t of redclaw production for 2011 in the Cultured Aquatic Species Information

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Programme, produced mainly in Morelos, Tamaulipas, Sinaloa, Baja California Sur, Puebla, and Veracruz. The National Fisheries Research Institute (INAPESCA, acronym in Spanish) published guidelines for the culture of *C. quadricarinatus* in Mexico, outlining 12 laws, norms, and regulations that affected management (DOF 2013). These did no limit imports of the species into Mexico. Nevertheless, the worldwide impact of diseases in the marine shrimp, *Penaeus vannamei*, culture (including WSSV and the Hepatopancreatic Acute Necrosis Syndrome) resulted in a crustacean imports prohibition in 2013 (CONAPESCA 2013). The National Service for health, safety, and agri-food safety has included live crustaceans and genetic material from any species in its prohibited import list for 2020 (SENASICA 2020).

To optimize production in Mexico, a significant effort has been done to improve knowledge on the biological requirements of *C. quadricarinatus*, including physiological response (Carreño-León et al. 2014), reproduction (García-Guerrero et al. 2003, Rodríguez-González et al. 2014), nutritional requirements (Cortés-Jacinto et al. 2005) and production (Naranjo-Páramo et al. 2004, Nuñez-Amao et al. 2018, 2019). As indicated above, the species was introduced to the country in few events, so the risk of inbreeding is significant. At commercial farms, broodstock for next cycle juvenile production is normally obtained during grow-out pond harvests by selecting 5-10% of the crop with the highest weight and good appearance. In the La Alberca farm in Michoacán, no size selection is carried out. Occasionally, feral organisms from local streams have been used (J. Naranjo, *pers. comm.*). After this selection, crosses occur randomly in reproduction ponds stocked at 1-4 m^{-2} and a female to male ratio of 3:1 (Naranjo-Páramo et al. 2004). It is important to notice that this artificial selection in production is not properly sustained by genetic information. As far as we know, there are no *C. quadricarinatus* genetic improvement programs in Mexico.

It is important to have an initial stock with broad genetic diversity to establish breeding programs. High genetic diversity is necessary to improve important economic traits such as growth, survival, or disease resistance (Davis & Hetzel 2000, Rao & Hodgkin 2002, Gjedrem & Baranski 2009). Moreover, it is necessary to avoid loss of genetic variability across generations, poor genetic management, such as the use of a small number of parents, small effective population size, kinship among breeders, or inadequate or uncontrolled mating that can lead to inbreeding (Allendorf & Ryman 1987, Gjerde et al. 1996, Gjerde & Rye 1998, Davis & Hetzel 2000, Doyle et al. 2001, Bentsen & Olesen 2002).

To detect changes in variability, monitoring of genetic diversity is necessary (Allendorf & Ryman 1987). To this end, microsatellite markers have been useful for aquacultured resources (e.g. Cruz et al. 2004, Zhu et al. 2006, Dixon et al. 2008, Sawayama & Takagi 2016, Napora-Rutkowski et al. 2017).

Few studies have focused on the genetic diversity in *C. quadricarinatus*. Baker et al. (2008) detected two divergent lineages in Australia's wild stock and two different lineages in Papua, New Guinea, using mitochondrial and microsatellites markers. He et al. (2012) evaluated genetic variability in three cultured redclaw crayfish lines in China with 28 microsatellite loci and reported moderate allelic diversity and moderate divergence between them. Jerry (2013) used six microsatellite loci to evaluate genetic diversity in different lines from commercial farms in Queensland, Australia. However, there are no genetic studies of redclaw crayfish populations in Mexico. Our goal was to assess the genetic diversity of divergent redclaw crayfish populations (three from farms in different locations and one feral population from an artificial water dam). Using microsatellite markers, determine possible genetic differentiation that would contribute to developing a founder stock with a wider genetic pool, suitable for the future development of a genetic improvement program.

MATERIALS AND METHODS

Sample collection

Generation 12 adult *Cherax quadricarinatus* individuals (weight, w = 60 ± 5 g, n = 56) were obtained from intensive culture 1000 m^2 high-density polyethylene (HDPE) lined outdoor ponds at BioHelis, the Innovation and Technology Park at the CIBNOR in La Paz, Baja California Sur, Mexico. Redclaw crayfish (w = 70 ± 8 g, n = 69) from semi-intensive clay-bottom 1000 m^2 ponds at El Vergel farm in Soto La Marina, Tamaulipas Mexico, and the Vicente Guerrero Dam (w = 77 ± 12 g, n = 69) were collected and air-shipped to La Paz. Individuals (w = 76 ± 7 g, n = 72) from an extensive clay-bottom farm (La Alberca) near Nueva Italia in Michoacán were also collected and air shipped to La Paz. Tissue samples from pleopods from all individuals were preserved in 80% ethanol. For comparison purposes, 50 juveniles (w = 1.5 ± 0.5 g) were collected and preserved in 80% ethanol from a research line recently imported from Australia at the University of Buenos Aires (UBA) in Argentina before shipped to CIBNOR. Further information on sampled populations is presented (Table 1).

Table 1. General information from populations of *Cherax quadricarinatus* evaluated in Mexico. A population recently introduced from Australia to Argentina was included as a reference. *Feral populations were established after accidental or intentional releases from local commercial farms. **According to Telchea & Fontaine (2014); 0: capture fisheries; 1: first trials of acclimatization to the culture environment; 2: part of the life cycle is completed in captivity, but several important bottlenecks still exist in others (e.g. reproduction, larval rearing); 3: the entire cycle is closed in captivity, but with wild inputs; 4: the whole life cycle is closed in captivity without wild inputs, but no selective breeding program is used; 5: a selective breeding program is used. UBA: University of Buenos Aires. CIBNOR: Northwest Biological Research Center.

Population	Location	Coordinates	Facilities	Culture Level	Domestication level**
CIBNOR	La Paz, BCS	24°08'05"N, 110°25'41"W	Pilot Scale	Intensive	4
La Alberca	Nueva Italia, Michoacán	18°52'27"N, 102°06'39"W	Farm	Extensive	2
Vicente Guerrero	Padilla, Tamaulipas	23°57'34"N, 98°39'57"W	Dam	Feral population*	0
El Vergel	Soto La Marina, Tamaulipas	23°45'20"N, 98°12'10"W	Farm	Semi-intensive	4
UBA	Buenos Aires	34°35'59"S, 58°22'23"W	Research	Experimental	3

Genetic analysis

Total DNA in all tissue samples was extracted with phenol-chloroform-isoamyl alcohol, following the protocol described by Wasko et al. (2003). Five microsatellite loci (Baker et al. 2000) were analyzed: CQU.0001, CQU.002, CQU.003, CQU.004, and CQU.006. Microsatellites were amplified by PCR in a 12.5 volume containing: 2 µl DNA, 1X Taq buffer, 3mM $MgCl_2$, 0.2mM dNTPs, 0.2µM of each primer Forward and Reverse, 0.02 U μL^{-1} Taq polymerase (Invitrogen). PCR thermal conditions were 4 min at 94°C of initial denaturation; continued by 33 cycles of 1 min at 94°C, 1 min at 55°C, 2 min at 72°C, and a final extension of 10 min at 72°C. PCR products were separated by electrophoresis in a 5% acrylamide 7.5 M urea gel; the alleles were visualized with Sybr Gold 10,000x (Invitrogen) in an FMBIO III scanner (Hitachi).

The number of alleles (Na), effective number of alleles (Ne), observed and expected heterozygosity (Ho and He), inbreeding coefficient (Fis), and allele frequencies were estimated with GenAlEx 6.503 (Peakall & Smouse 2012). Genetic differences between lines, measured as Wright's Fst values, were calculated by Arlequin 3.5 (Excoffier & Lischer 2010). The statistical significance of each comparison was estimated through 10,000 permutation procedures. Also, we used GenAlEx 6.503 (Peakall & Smouse 2012) to calculate a pairwise genetic distance matrix and then converted it to a covariance matrix to perform a principal coordinate analysis (PCoA). Further, we perform an AMOVA with 999 permutations to estimated genetic variation between and within the population. We used organisms with a minimum of four genotyped loci microsatellites; individuals with two or more missing data were discarded.

RESULTS

A genetic diversity value for all groups is summarized in Table 2. Na ranged from 2.8-8.8 and Ne from 1.588-3.944; in both cases, the UBA group showed a higher number of alleles and presented higher Ho and He values (0.600 and 0.695, respectively). For Mexico, the El Vergel group had a higher Na (6.2), and Vicente Guerrero had a higher Ne (3.219). CIBNOR showed the lowest diversity. The Fis values were 0.081 to 0.193; UBA showed the lowest Fis and La Alberca's highest value.

Allele frequencies (Fig. 1) revealed private alleles and different allele frequencies in the groups, mainly for locus CQU.006. For locus CQU.001 and CQU.002, similar alleles and frequencies were shown in all groups, except for UBA.

Genetic differentiation analysis based on pairwise Fst (Table 3) showed that all lines are statistically different Fst ($P < 0.05$). The highest degree of differentiation occurred between CIBNOR and UBA (0.33213). On the other hand, the lowest degree of differentiation occurred between La Alberca and El Vergel (0.04662), followed by El Vergel and Vicente Guerrero (0.08270). In general, CIBNOR presented the greatest Fst values when compared to the other Mexican groups.

Principal coordinate analysis (PCoA) (Fig. 2) confirmed the genetic differences among individuals from CIBNOR and, as expected, from UBA. The accumulated percentage of variation explained by the three first axes was 33.61%. The first axis explained 13.05%, the second 10.60%, and the third 9.96%. The AMOVA results showed a percentage of molecular variance of 15% among populations, 26% between individuals, and 59% within individuals.

Table 2. Genetic diversity of *Cherax quadricarinatus* from populations in Mexico. n: number of individuals analyzed, Na: average number of alleles, Ne: effective number of alleles, Ho: observed heterozygosity, He: expected heterozygosity, Fis: inbreeding coefficient. A recently introduced population from Australia to Argentina was included for reference values. UBA: University of Buenos Aires. CIBNOR: Northwest Biological Research Center.

	n	Na	Ne	Ho	He	Fis
CIBNOR	56	2.8	1.588	0.321	0.357	0.095
La Alberca	66	4.0	1.948	0.355	0.466	0.193
Vicente Guerrero	59	5.4	3.219	0.419	0.553	0.159
El Vergel	64	6.2	2.927	0.467	0.595	0.186
UBA	33	8.8	3.944	0.600	0.695	0.081

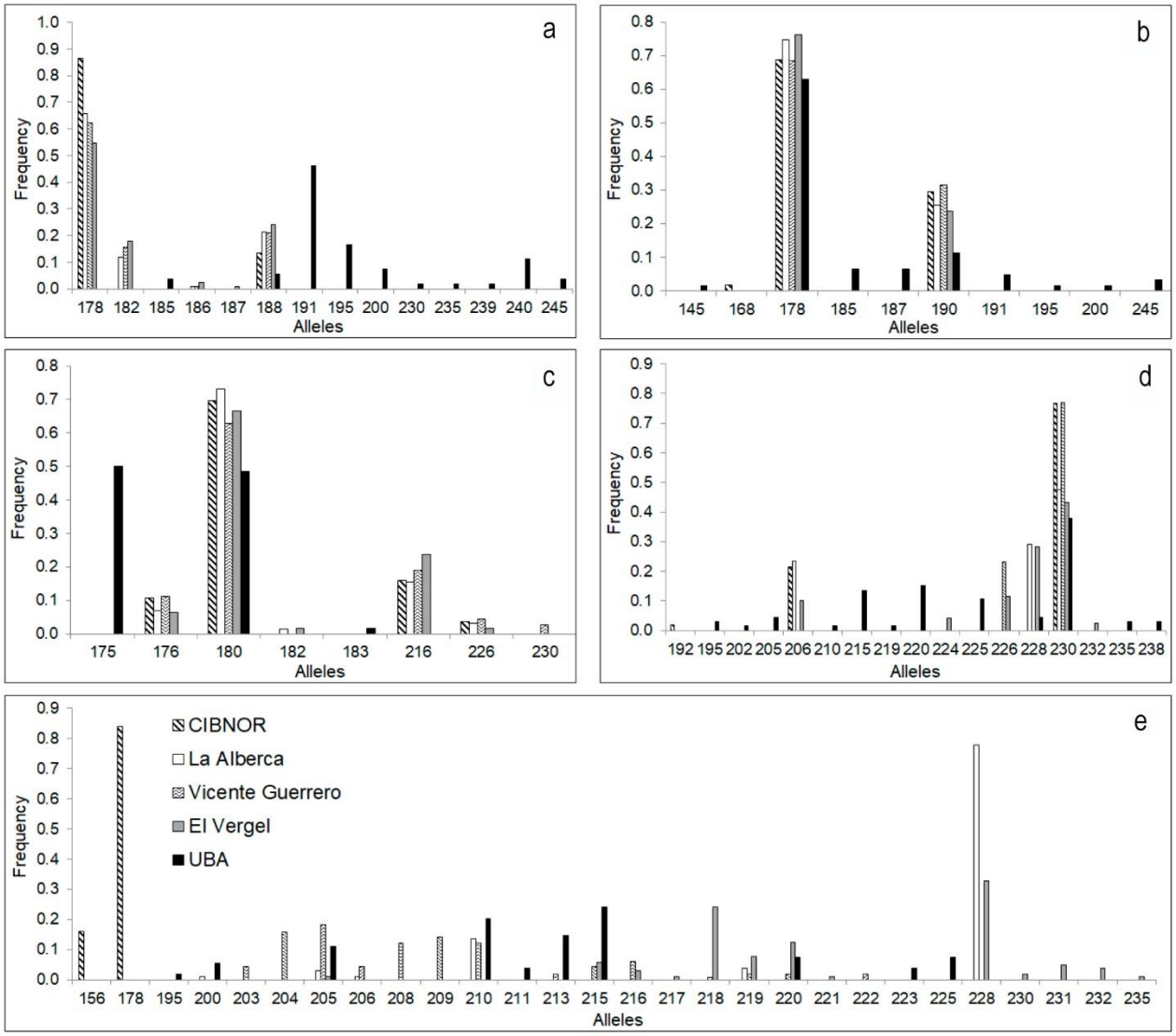

Figure 1. Allele frequencies for the five microsatellite loci in *Cherax quadricarinatus* populations. a) Locus CQU.001, b) locus CQU.002, c) locus CQU.003, d) locus CQU.004, e) locus CQU.006. Northwest Biological Research Center (CIBNOR) n = 56; La Alberca n = 66; Vicente Guerrero n = 59; El Vergel n = 64; UBA; University of Buenos Aires (UBA) n = 33.

Table 3. Pairwise population Fst values for divergent *Cherax quadricarinatus* populations. All pairwise Fst values are statistically significant ($P < 0.05$). UBA: University of Buenos Aires. CIBNOR: Northwest Biological Research Center.

	CIBNOR	La Alberca	Vicente Guerrero	El Vergel	UBA
CIBNOR	*				
La Alberca	0.25328	*			
Vicente Guerrero	0.20161	0.14015	*		
El Vergel	0.21585	0.04662	0.08270	*	
UBA	0.33213	0.23926	0.17259	0.17299	*

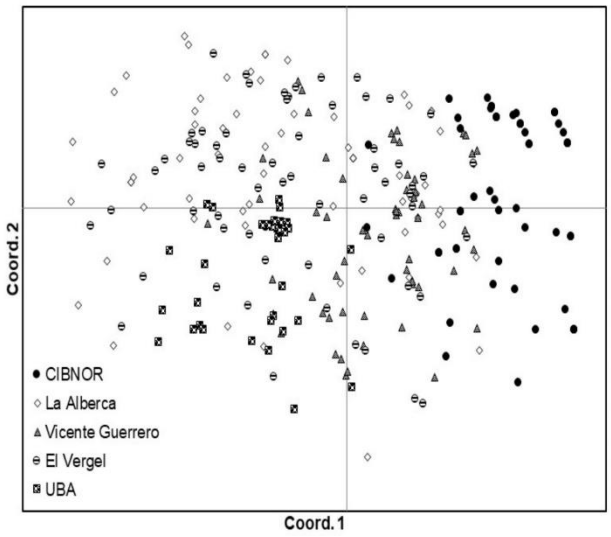

Figure 2. Principal coordinate analysis (PCoA) plot for different *Cherax quadricarinatus* populations in Mexico. A recently introduced population from Australia to Argentina was included as a reference. UBA: University of Buenos Aires, CIBNOR: Northwest Biological Research Center.

DISCUSSION

In our study, Na's terms' genetic variability was from low to moderate (2.8-6.2) for the divergent groups in Mexico, with an average of 4.6 alleles. The mean value for UBA was 8.8, which is probably related to a more recent translocation event, with a potential different bottleneck effect and subsequent genetic drift or a more efficient management strategy to prevent the loss of genetic variability. The moderate genetic variability in the Mexican lines agrees with previous reports in cultured lines of the redclaw in Australia and China (He et al. 2012, Jerry 2013) and is lower than that reported for Australian and Papua New Guinean wild stocks (Baker et al. 2008) that ranged from 11 to 40 alleles.

Jerry (2013) analyzed the genetic variability in eight Australian farms and the "Walkamin" genetic line (Jones et al. 2000) from the Queensland Department of Primary Industries (QDPI), using six microsatellite loci from Baker et al. (2000), evaluating the results for the five microsatellite loci we used, the Na ranged from 2.5 to 7, similar to our study results (Na 2.8-6.2). He et al. (2012) reported a range of 2.96 to 3.25 alleles for three cultured lines in China, using 28 microsatellite loci, which is similar to the results for CIBNOR (Na 2.8). Ho in our study (0.321-0.600) was within the range of Australian farms (0.32-0.78; Jerry 2013) and lower than the report of He et al. (2012) for China (0.65-0.68). Significantly, wild stocks' values ranged from 0.35 to 0.71 (Baker et al. 2008), showing high variability. It is important to state that heterozygosity is not a perfect genetic variation indicator (Cruz et al. 2004). It is not sensitive to Na since high values with as few as two alleles can be obtained (Beardmore et al. 1997). A more appropriate evaluation of genetic variability must consider both Na and Ho to avoid risky or erroneous conclusions. In terms of genetic variation, the Mexican lines have moderate genetic variation, enough to proceed to a cross-mating design that generates a broodstock nucleus with wider genetic variation, as was previously done in Australia (Jerry 2013).

The genetic differentiation analysis showed that all lines were statistically different based on pairwise Fst ($P < 0.5$), despite the common events of introduction in the case of Mexico (Ponce-Palafox et al. 1999), with a similar origin two decades ago. It possibly indicates a differential effect of the genetic drift, different effective number of breeders, and directed or non-directed breeding. CIBNOR showed the larger Fst values, particularly when compared with UBA (0.33213). The PCoA plot shows a tendency in which individuals from CIBNOR separate from individuals from other groups. CIBNOR is the only group properly domesticated for the Mexican lines, managed and studied, with reported intentions of developing a nucleus with wide variability that leads to a genetic selection program (Mora-Castrejón 2019).

Despite being considered a feral population, crayfish from the Vicente Guerrero dam showed similar diversity to the nearby El Vergel farm and lower than the Argentinean sample. Though *C. quadricarinatus* is susceptible to escapes from captivity due to its ability to climb and move out of the water (Jones et al. 2000), the source of the feral population in Vicente Guerrero

dam is probably the intentional releases from nearby farms (Mendoza-Alfaro et al. 2011). Pairwise Fst analysis showed the low genetic distance between El Vergel farm and the Vicente Guerrero dam (0.08270), both in Tamaulipas.

CIBNOR showed the lowest diversity, underlining the need to increase genetic diversity. Inbreeding accumulates over time in cultured populations since related individuals will mate, even with best management practices securing random pairings (Andersen & Hayes 2005). Improper husbandry can accelerate the loss of genetic variation. Considering that, the overall objective of evaluating diverging lines is to establish a founder stock with wider genetic variation and significant capacity for domesticated management in aquaculture systems. The results of genetic variation and previous production performance (Hernández-Gurrola et al. 2020) reveal that the CIBNOR (generation 12) line is appropriate for founder stock cross-breeds with individuals from the other evaluated lines in Mexico.

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