

ASSESSING THE GENETIC DIVERSITY AND GENE FLOW OF POPULATIONS OF THE CRAB *UCIDES CORDATUS* (DECAPODA: OCYPODIDAE) ON THE BRAZILIAN COAST USING MICROSATELLITE MARKERS

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ABSTRACT

The variation in five microsatellite loci was used to estimate the genetic structure and demographic parameters of the mangrove crab, *Ucides cordatus* (Linnaeus, 1763), based on 365 individuals from nine locations throughout the Brazilian coast. There was considerable variability in the studied fragments, with high values of expected heterozygosity and evidence for weak genetic structure between some of the samples and regions, despite vast geographical distances between them. F_{ST} values involving the Amapá sample were near zero, indicating that the estuary of the Rio Amazonas mouth does not represent a barrier to dispersal of this species. However, the highest levels of genetic divergence involve the southernmost sample (Paraná, $F_{ST} = 0.03$).

KEY WORDS: estuary, gene flow, larval dispersion, migration, *Ucides cordatus*

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INTRODUCTION

Ucides cordatus (Linnaeus, 1763) is a semi-terrestrial crab that inhabits mangroves in the western Atlantic Ocean. This species has great economic and social importance in Brazil and populations of several locations has drastically reduced due either to overfishing (Dias-Neto, 2010), or to an emerging disease known as the Lethargic Crab Disease (Boeger et al., 2005). This is an iteroparous species, with overlaps generations. The sexual maturation is achieved at three years old. Adults are completely dependent of estuaries, especially of Mangrove forests, but larvae are partially dependent of open sea water (Dias-Neto, 2010). A pattern of larval exportation was found in two distinct estuaries in northern and northeastern Brazil (Silva-Falcão et al., 2007; Simith and Diele, 2008). However, the interaction of larval biology and physiographic factors of different estuaries has never been explored.

The species has been subject to studies on population-genetics along the coast of Brazil, as an attempt to provide information useful for the definition of conservation strategies. None or very low genetic structure was detected along great part of the Brazilian coast based on different molecular markers, i.e., RAPD and PCR-RFLP (Oliveira-Neto et al., 2007a, b) and D-loop sequences (Oliveira-Neto et al.,

2007a). This result is concordant with the reproductive strategy of larval exportation. However, the validity of these results for entire Brazilian coast has been questioned even the lack of genetic structuring occurring in other species of marine brachyurans, including *Pachygrapsus crassipes* (Randall, 1840) (cf., Cassone and Boulding, 2006), *Callinectes sapidus* Rathbun, 1896 (cf., McMillen-Jackson and Bert, 2003), *Callinectes bellicosus* (Stimpson, 1859) (cf., Pfeiler et al., 2005), and *Cardisoma guanhumi* Latreille, 1825 (cf., Oliveira-Neto et al., 2008). The existence of species with dispersion capacity apparently similar or higher than that of *U. cordatus* that depict moderate genetic structure in genetic diversity, e.g., *Callinectes danae* Smith, 1869 along the southern Brazilian coast (Weber and Levy, 2000), *Carcinus maenas* (Linnaeus, 1758) along the Europe coast (Roman and Palumbi, 2004), requires further investigation.

The lack of genetic structure may be associated to limitation of genetic marker or insufficient sample size necessary to detect weak structure. To prevent this factors, we tested the genetic structuring of *U. cordatus* in the coast of Brazil increasing the sampling effort (sites and individuals per site) and utilizing microsatellite markers, a method considered more sensitive than the previously applied in similar studies with the species (Oliveira-Neto, 2007a, 2008) because they

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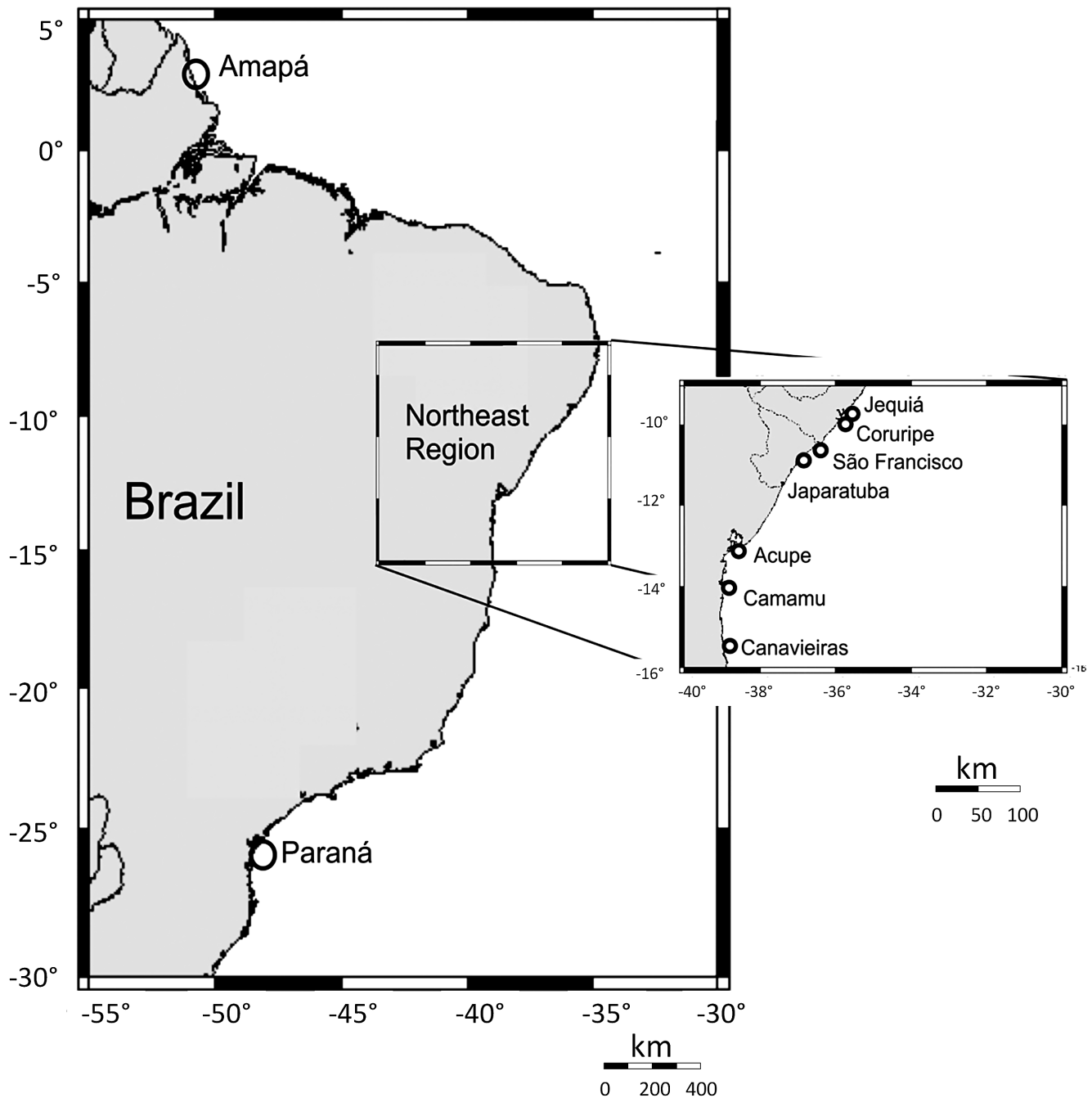


Fig. 1. Sample sites located in Brazilian coast: North (Amapá), Northeast region (seven sites), and South (Paraná).

are nuclear, co-dominant and independent markers. For instance, microsatellite markers allowed detection of weak genetic structure of many invertebrates populations in Atlantic Ocean and, in particular, in population of the shrimp *Litopenaeus schmitti* (Burkenroad, 1936) from the south/east and the north/northeast coasts of Brazil (Maggioni et al., 2003).

A potential barrier to dispersion of *U. cordatus* could be tested adding a sample located northern Amazon River mouth. Amazon River Estuary has been appointed as a geographical barrier for many species and may be very different even when comparing species of the same genus (Rocha et al., 2002). The amount of freshwater and fine

sediment discharged by Amazon River into the sea are much greater than any other river in the world (Meade et al., 1985; Degens et al., 1991), turning adjacent open sea and beaches very similar to an usual estuary (Allison and Lee, 2004). These circumstances may facilitate larval sedimentation of *U. cordatus* in an appropriated ecosystem. However, the effect of currents and water characteristics in distribution and survival of larvae are unknown. Finally, we intend to clarify the intensity of genetic structuring in a large geographical scale, including a potentially strong dispersion barrier and increasing significantly the statistical power including more individuals and nuclear loci.

Table 1. Heterozygosity values and R_{ST}/F_{ST} values from nine *U. cordatus* populations, using microsatellites loci. *Significant after Bonferroni correction ($p < 0.0014$). **Significant $p (< 0.001)$ in Exact test of non-differentiation. AP = Amapá, JE = Jequiá, CO = Coruripe, SF = São Francisco, JA = Japarutuba, AC = Acupe, CA = Camamu, CN = Canavieiras, PR = Paraná.

	AP	JE	CO	SF	JA	AC	CA	CN	PR
Sample size	19	38	32	58	77	20	40	16	73
Observed heterozygosity									
Mean	0.72	0.69	0.79	0.73	0.80	0.73	0.72	0.77	0.69
s.d.	0.17	0.28	0.24	0.18	0.15	0.22	0.19	0.21	0.12
Expected heterozygosity									
Mean	0.73	0.70	0.73	0.76	0.76	0.68	0.69	0.76	0.73
s.d.	0.13	0.20	0.17	0.11	0.10	0.19	0.12	0.12	0.10
F_{ST}									
AP									
JE	0.02								
CO	0.01	0.00							
SF	0.02**	0.02*	0.00						
JA	0.01	0.01	0.00	0.00**					
AC	0.04	0.01	0.00	0.01**	0.00				
CA	0.02	0.02**	0.01**	0.01**	0.01	0.01			
CN	0.00	0.00	0.00	0.00	0.00	0.00	0.00		
PR	0.03*	0.03*	0.02*	0.01**	0.01	0.03*	0.02*,**	0.00	

MATERIAL AND METHODS

We collected samples from nine localities along the Brazilian coast (Fig. 1, Table 1). A pereopod of each crab was removed; the muscle was preserved in NaCl-EDTA-DMSO buffer (Seutin et al., 1991). Total DNA was extracted using the Charge Switch Kit (Invitrogen®). Five loci described by Baggio et al. (2011) (A5, A11, A120, B124 and C109) were used to genotype all individuals. Polymerase chain reactions (10 μ l) were performed with the following final concentration: 1 \times reaction buffer, 2 mM MgCl₂, 0.2 mM DNTP, 0.6 μ M of each primers, 0.025 U/ μ l *Taq* and 1.5 ng/ μ l template DNA. We obtained the amplification of target fragments in a thermal-cycler Eppendorff using the following program: initial denaturation at 94°C for 3 min, followed by 35 cycles of denaturation at 94°C for 40 seconds, annealing for 40 seconds and extension at 72°C for 30 seconds. The process was completed with a final extension at 72°C for 40 minutes. Annealing temperatures follow protocol reported by Baggio et al. (2011). Products were genotyped in an automatic sequencer ABI 3130. The fragments size was determined in the software GeneMarker 1.6 (SoftGenetics).

We tested the potential presence of null alleles and scoring errors due to stuttering and large allele drop-out using MICRO-CHECKER 2.2.3 (van Oosterhout et al., 2004). Allele frequencies and measurements of genetic diversity, such as expected heterozygosity (H_E), observed heterozygosity (H_O), number of alleles (N_A) and allelic richness (A), were calculated in Arlequin 3.1 (Excoffier et al., 2005). For each sample site, we tested the Hardy-Weinberg equilibrium applying 1×10^6 steps in the Markov chain and 1×10^5 steps of dememorization. The resulting data set was initially analyzed taking into account all loci and then removing loci that deviated from the Hardy-Weinberg equilibrium. From the frequency of alleles for each sample, we obtained values of R_{ST} (Slatkin, 1995) and F_{ST} using 2×10^4 permutations for significance calculation. Mantel test was used to test the correlation among genetic differentiation (R_{ST}) and geographical distance. In addition, we performed the Analysis of Molecular Variance (AMOVA, Excoffier, 2004), separating the populations in the groups North

(AP, Amapá), Northeast (JE, Jequiá; CO, Coruripe; SF, San Francisco; JA, Japarutuba; AC, Acupe; CA, Camamu; CN, Canavieiras) and South (PR, Paraná). All these tests were processed with the program Arlequin 3.1 (Excoffier et al., 2005), using Bonferroni corrections for the multiple statistical tests.

The simulation procedure of Ryman et al. (2006) implemented in the software POWSIM version 4.0 (Ryman and Palm, 2006) was used to assess the alpha error and statistical power of our microsatellite loci to detect an actual level of divergence ($F_{ST} = 0.02$) using different combinations of sample and the allele frequencies from the current data set. Each simulation was run 1000 times and power was determined as the proportion of simulations that Fisher's exact test detected significant at the 0.05 level.

RESULTS

We genotyped 365 specimens of *U. cordatus* resulting in 109 alleles (average of 21.8 alleles per locus) (Table 3). The B124 and A5 loci depicted the highest allelic diversity, with 33 and 32 alleles, respectively. Only 13 alleles were found for C109 locus. The mean expected heterozygosity in each locus ranged from 0.54 to 0.90, but did not present significant differences among estuaries. No scoring errors associated to stuttering or null alleles was identified. Two of the 5 examined loci were slightly deviated from the Hardy-Weinberg equilibrium (C109 and A5). Power simulations indicated that most data sets were sufficiently informative to detect a significant F_{ST} as low as 0.02 among smaller sample sizes and 0.01 among clustered samples.

We found weak signal of geographic structure in the genetic diversity in all sampling sites using AMOVA ($F_{ST} = 0.013$, $p = 0.000$) (Table 4). The AMOVA also revealed that the largest percentage of variation was due primarily to the variation contained within populations (98.9%). Pairwise R_{ST} were no significantly different from zero in all comparisons. However, F_{ST} values (Table 1) were very low and no significantly different from zero after Bonferroni correction in almost all pairwise populations comparisons but statistically significant between the subpopulation of Paraná and those of Amapá ($F_{ST} = 0.03$; $p < 0.001$), Jequiá ($F_{ST} = 0.03$; $p < 0.001$), Coruripe ($F_{ST} = 0.02$;

Table 2. Pairwise differentiation comparisons (* $p < 0.001$, ** $p < 0.05$ in Exact test of non-differentiation) among four geographic regions. North = Amapá, G1 = JE + CO + SF + JA, G2 = AC + CA + CN, South = Paraná.

	Group	North	G1	G2	South
F_{ST}	G1	0.015*		0.002	0.015**
	G2	0.018*			0.017**

Table 3. Characterization of alleles diversity among four geographic regions. North = Amapá, G1 = JE + CO + SF + JA, G2 = AC + CA + CN, South = Paraná.

	Locus	North	G1	G2	South	Total
Number of alleles	1	9	28	21	12	33
	2	5	13	8	10	15
	3	5	14	11	8	16
	4	3	9	5	5	13
	5	10	29	19	20	32
Mean		6.4	18.6	12.8	11.0	21.8
s.d.		3.0	9.2	6.9	5.7	8.8
Range of allele sizes	1	19	47	79	26	79
	2	8	26	12	98	106
	3	14	22	20	14	22
	4	28	41	45	27	61
	5	15	32	33	28	33
Mean		16.8	33.6	37.8	38.6	60.2
s.d.		6.6	9.3	23.5	30.1	30.5
Expected/observed heterozygosity	1	0.80	0.84/0.80	0.77/0.79	0.71/0.65	0.81
	2	0.72	0.56/0.55	0.53/0.53	0.67/0.76	0.60
	3	0.52	0.65/0.58	0.61/0.52	0.69/0.64	0.64
	4	0.54	0.51/0.46	0.48/0.44	0.57/0.50	0.52
	5	0.86	0.90/0.86	0.88/0.82	0.90/0.85	0.90
Mean		0.69	0.69	0.65	0.71	0.70
s.d.		0.15	0.17	0.17	0.11	0.14

$p = 0.001$), and Acupe ($F_{ST} = 0.04$, $p < 0.001$) (Table 1). Two adjacent estuaries of Northeastern region showed statistically significant divergence ($F_{ST} = 0.02$, $p < 0.001$). F_{ST} values were not directly proportional to geographical distances among compared localities ($p = 0.21$). The Exact test of non-differentiation showed significance between sample with a great number of individuals and not present concordance with precedent analysis. Comparing the geographically extreme samples with two grouped sampled of Northeastern region revealed that F_{ST} values became even lower than in precedent analysis. However, the differences were statistically significant (Table 2).

Detailed tabulations concerning gene frequency and haplotype data are available from the authors on request.

DISCUSSION

The microsatellite analysis confirms the high genetic diversity in populations of *U. cordatus* detected in other studies using distinct molecular markers (Oliveira-Neto et al., 2007a, b). This scenario is likely the consequence of a large

population size that has been under expansion for thousands of years, without severe bottleneck events since the Pleistocene era. The very low and/or non-significant population genetic structuring, as reported in these studies, is supported also by our results. The increase in sample size contributed to an increase in the number of significant cases genetic structuring, but not contributed to the increase of F_{ST} . The lack of correlation between geographical distance and R_{ST} values detected herein was observed previously in other *Brachyura* species elsewhere in the world (McMillen-Jackson and Bert, 2003; Cassone and Boulding, 2006).

The present and previous studies (Oliveira-Neto et al., 2007a, b) on the population genetic of *U. cordatus* corroborate that larvae are intensely exchanged between estuaries. However, the intensity of the gene flow observed for *U. cordatus* is exceptional, even when compared with animals that exhibit similar reproductive strategies. Variable levels of genetic structure were detected for six species of shrimps in the Brazilian coast, varying from not structured to completely structured (cryptic species) (Gusmão et al., 2000, 2005; Maggioni et al., 2003; Voloch and Solé-Cava,

Table 4. Results of AMOVA analysis from nine samples of *U. cordatus*, using 5 microsatellite loci.

Source of variation	df	Sum of squares	Variance of components	Percentage of variation	Index value	p
Among groups	3	13.0	0.01 Va	0.81		
Among populations within groups	5	11.2	0.01 Vb	0.52		
Within populations	739	1179.7	159.6 Vc	98.67		
Total	747	1204.0	161.8			
F_{IS}					0.020	0.068
F_{ST}					0.013	0.000
F_{CT}					0.008	0.031

2005). Thus, geographical features that represent a dispersal barrier for many species in the southwestern Atlantic Ocean are not shared by the populations of *U. cordatus*. For instance, Rocha (2003) suggested that the role of the putative geographical barrier represented by the Amazon River delta has been overestimated for some animal species. Indeed, the only sample of this study located northern of the Amazonas River delta showed no differentiation from the remaining subpopulations, even when compared to the sample of Paraná, distant more than 5000 km.

The genetic diversity of *U. cordatus* is consistent with its life-cycle strategy. The release of larvae by female crabs occurs almost synchronically, during highest tide (Silva-Falcão et al., 2007; Simith and Diele, 2008). The cloud of larvae is probably carried out from the estuarine mangrove areas into coastal water, mainly by tidal superficial currents, similarly *C. sapidus* (Tilburg et al., 2009). Coastal superficial currents have great temporal and spatial variation in their direction (Miranda, 1970; Mesquita and Hatari, 1971; Silva et al., 2005) and likely promote initial disruption and dispersion of the larval cloud into distinct directions. The cloud may disperse far into the open sea, being collected up to 400 km distant from the coast. As the larvae develop into later stages, it sinks deeper being exposed to currents of distinct directions. These processes likely maximize the spreading of larvae in every direction, which reach and colonize distinct estuaries promoting homogenization of the genetic profile of local and regional populations. This pattern of larval dispersion probably allows the exchange of larvae between estuaries located in both sides of a potential gene-flow barrier. Further, considering the scenario above the stepping-stone model (Hastings and Harrison, 1994) for the colonization of estuaries is unlikely, because dispersion distances are much larger than mean distance of adjacent estuaries. The scenario above strongly supports that restocking of a certain estuary is most likely not accomplished by larvae produced locally.

This random dispersal of larvae of *U. cordatus* is likely responsible by the transposition of important geographical barriers for other species. For instance, climatologic currents of the northwestern Brazilian coast were considered by Pil et al. (2011) an important geographical barrier for the dispersion of propagules of *Rhizophora mangle*. Climatologic currents are superficial and apparently greatly influence the dispersal of the floating propagule. However, since later larval stages of *U. cordatus* position themselves in deeper waters, they are likely capable of “transposing” the climatologic currents carried by contrary deeper oceanographic currents.

Concluding, the low levels of genetic structure observed in this study suggest that gene flow is intense between Brazilian estuaries, even between those separated by thousands of kilometers. The weak genetic structure found in this population may be caused both by geographical distance and local physiographic factors.

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