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Lack of population genetic structure among Brazilian populations of *Callinectes danae* (Brachyura: Portunidae): implication for management and conservation

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ABSTRACT

Recognizing genetic stocks can guide efficient management efforts for fisheries. This would guarantee sustainable exploitation of present fisheries, assist the recovery of depleted ones, and ensure the maintenance of different genetic lineages for the target species. The swimming crab *Callinectes danae* Smith, 1869 is an economically important species for several local western Atlantic coastal populations. This species can be found along all the Brazilian coast occurring in shallow waters. Considering the importance of this species, we investigated the presence of genetic stocks along its distribution aiming to provide information for fishery management. We used two mitochondrial markers (COI and 16S) to characterize individuals from many fishing areas comprising approximately 7000 km of extension. Our results indicate lack of genetic structure among populations of *C. danae* and signs of high connectivity. This scenario is probably result of great dispersal capability and tolerance for different marine environments. Therefore, *C. danae* is characterized as a single genetic stock along the Brazilian coast and future management should consider country-level plans.

1. Introduction

Overfishing is recognized as one of the main causes of natural population collapses (Pauly et al., 2002). This activity may cause direct and indirect impacts in the ecosystems by interfering on trophic network and impacting biodiversity due to local extinction of species (Lewison et al., 2004). Thus, fisheries management is a key aspect since its major goal is to guarantee sustainable exploitation of present fisheries and to assist the recovery of depleted ones (Ward, 2000).

A key concept when dealing with conservation and management is the recognition of stocks (Cope and Punt, 2009). Stocks are the resource unit and can be defined as a local population of an exploited species in a determined area — the fishery stock (Smith et al., 1990). This definition might not be accurate to identify meaningful biological units. Thus, a stock can also be defined as an intraspecific group of randomly mating individuals with temporal and spatial integrity (Ihssen et al., 1981). Molecular markers, in this sense, can help us to identify panmictic groups and delimitate their distribution, defining a genetic stock [Waples et al., 2008, but see Begg and Waldman (1999) for more approaches to identify stocks]. There should be genetic homogeneity within a stock, but it may occur genetic divergence among stocks (Thorpe et al., 2000). For instance, the highly commercial fish species *Euthynnus affinis* is considered as a single genetic stock along the Indian coast, considering D-loop marker because there is no differentiation among sampled locations (Kumar et al., 2012). Contrastingly, the molecular markers COI and 16S identified two genetic stocks within the red and blue shrimp *Aristeus antennatus*, a deep-sea fishery, from two different regions in the Western Mediterranean (Fernández et al., 2011). Both examples represent the use of different markers for the detection of genetic stocks along their distribution within the species level.

Management and conservation measures should take genetic stocks into consideration because each scenario demands different decisions (Waples et al., 2008; Reiss et al., 2009). For instance,

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if there is more than one genetic stock, one should aim to treat each one of them as different management and conservation units. This strategy would guarantee that fisheries impact as little as possible over intraspecific genetic diversity. Contrastingly, the identification of a single stock along the whole space distribution range of a target species can imply a common management strategy in all localities. Therefore, determining genetic stocks can support deciding adequate management strategies for a specific fishery resource (Waples et al., 2008; Reiss et al., 2009).

The genus *Callinectes* Stimpson, 1860 encompasses 15 species of commercially important swimming crabs, of which most (13) occur on the Pacific and Atlantic coasts of the Americas (Robles et al., 2007; WoRMS Editorial Board, 2020). Members of this genus represent an annual catch of around 200,000 t and 2000 t for *Callinectes sapidus* Rathbun, 1896 and *Callinectes danae* Smith, 1869, respectively, in the western Atlantic (FAO 1950–2017 Global Capture Production in FAO, 2019). In Brazil, *Callinectes* swimming crab's fishery activity has its origin in bycatch fauna from shrimp fishery (Keunecke et al., 2008), or in artisanal fishery (Sforza et al., 2010). One of us (FLM) have also noted an increase in catches during periods of prohibition on fishing for more profitable species, such as commercial shrimps. These swimming crabs are commonly found in local markets along the coast, especially sold as ''packed meat'', representing an important economic resource for local coastal human populations (Jablonski et al., 2006). *Callinectes danae* is one of the most prevalent swimming crabs in shallow and coastal areas. It is abundant in estuaries, mangroves, and on the continental shelf down to 70 m, and from brackish to hypersaline environments (Norse, 1978; Buchanan and Stoner, 1988; Melo, 1996; Andrade et al., 2015), occurring in the western Atlantic Ocean, from Florida to Argentina (Williams, 1974; Mantelatto and Fransozo, 2000; Chacur and Negreiros-Fransozo, 2001). Even though we have information about their ecology and reproductive patterns (Costa and Negreiros-Fransozo, 1998; Sant'Anna et al., 2012), few efforts have been made to delimitate genetic stocks.

Here we investigated genetic structure of *C. danae* along the Brazilian coast (∼7000 km) using two mitochondrial markers (the barcoding region of the COI gene and a fragment of the 16S rRNA), which have been used in management and monitoring studies on decapods (Marra et al., 2015; Rumisha et al., 2017; Buranelli et al., 2019). We performed molecular analyses aiming to first confirm that *C. danae* individuals from Brazil represent a single species, and then to identify possible different genetic units within this species (different genetic stocks). The outcomes of this study provide useful information for management of this fishery along a wide range of its distribution in the western Atlantic Ocean.

2. Materials and methods

2.1. Sampling

Sampling was focused on obtaining *C. danae* from across all the Brazilian coast, comprising a range of approximately 7000 km (Fig. 1, Table 1). Specimens were obtained from the Coleção de Crustáceos do Departamento de Biologia (CCDB), Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto (FFCLRP) – Universidade de São Paulo (USP); Coleção Científica de Crustáceos Decápodes do Laboratório de Crustáceos Decápodes (LCD/CCCD), Programa de Pós-Graduação em Aquicultura, Instituto de Oceanografia – Universidade Federal do Rio Grande (FURG); Museu de Zoologia (MZUSP) – Universidade de São Paulo (USP), or were collected directly in the field. All specimens were preserved directly in 80%–90% ethanol (ETOH), and crabs were identified based on morphological characters (Williams, 1974; Melo, 1996).

2.2. DNA extraction, PCR amplification, and sequencing

DNA extraction, amplification and sequencing protocols followed Schubart et al. (2000a) with modifications according to Mantelatto et al. (2018). Total genomic DNA was extracted from muscle tissue of the chelipeds, preferentially from the articulation between the carpus and merus. Muscle tissue from each individual was incubated for 1–12 h in 600 μL of lysis buffer and 200 μL of proteinase K (500 μg/μL) at 55 °C; protein was separated by the addition of 200 μL of 7.5 M ammonium acetate before centrifugation. DNA was precipitated by the addition of 600 μL of cold absolute isopropanol, followed by centrifugation; the resultant pellet was rinsed with 70% ethanol, dried and resuspended in 10–20 μL of TE buffer.

PCR reactions were performed in 25 μl volumes (200 μM each dntp, 1 × buffer, 0.5 μM each primer, 1 unit Taq polymerase, 1 μl extracted DNA diluted to comprise ∼50 ng). A ∼700-base-pair (bp) region of the COI gene was amplified from diluted DNA by means of polymerase chain reaction (PCR) in a Thermo (Portsmouth, NH, USA) PxE0.2 ThermalCycler (temperature profiles included an initial denaturing for 2 min at 94 °C followed by 35 cycles of 30 s at 94 °C, 30 s at 50 °C, and 1 min at 72 °C. A final extension of 2 min at 72 °C was added to ensure complete elongation) using the primers: COH6 (5′-TADACTTCDGGRTGDCCAARAYCA-3′) and COL6b (5′-ACAAATCATAAAGATATYGG-3′) (Schubart and Huber, 2006). A region with ∼600 bp of the 16S RDNA gene was amplified (temperature profiles included an initial denaturing for 5 min at 95 °C followed by 40 cycles of 45 s at 95 °C, 30 s at 46 °C, and 1 min at 72 °C. A final extension of 3 min at 72 °C was added to ensure complete elongation) with the primers designated as follows: 16SH2 (5′-AGATAGAAACCAACCTGG-3′) and 16SL2 (5′-TGCCTGTTTATCAAAAACAT-3′) (for references on the primers see Schubart et al., 2000a,b). PCR products were purified using the kit SureClean Plus and sequenced with the ABI Big-Dye Terminator Mix (Applied Biosystems, Carlsbad, CA, USA) in an ABI Prism 3100 Genetic Analyzer (Applied Biosystems automated sequencer) following Applied Biosystems protocols. All sequences were confirmed by sequencing both strands.

Sequences editing and *de novo* assembling were performed in Geneious v11.1.4 using default settings and visually checked (Kearse et al., 2012). Sequences alignment was performed in MAFFT v.7 (Katoh and Standley, 2013), which resulted in final alignments of ∼550 bp for 16S RDNA and ∼650 bp for COI mtDNA.

2.3. Genetic diversity, genetic structure and genetic distance

We organized our dataset in two ways aiming to identify if fisheries stocks (Smith et al., 1990) represent different genetic stocks (Waples et al., 2008). First, each Brazilian state was considered as one fishery stock. Second, each geographical region from the Brazilian coast (South, Southeast, Northeast, North) as one fishery stock (Table 1). We decided to proceed with these two datasets aiming to depict the scenario for future fisheries management and conservation in different areas along the Brazilian coast. Even though there is no systematic review on the profile and intensity of bycatch fauna and artisanal crab fishery along the Brazilian coast, we are aware that there might be differences due to alternative activities for fishers (Lopes et al., 2011), and local political rules (Begossi, 2006). In this sense, analyses were performed considering both datasets.

Genetic diversity indices – haplotype number, polymorphic sites, haplotypic diversity, and nucleotide diversity – were computed using DNASP v.4.10.9 (Rozas and Rozas, 1999) for both genes.

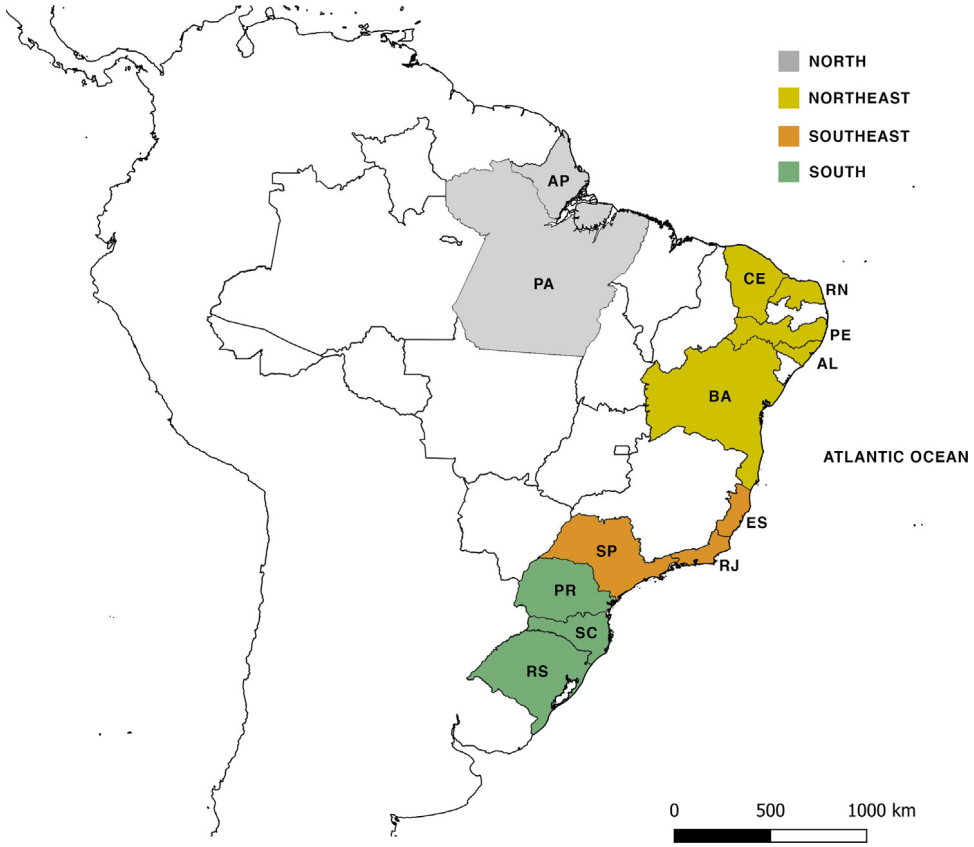

Fig. 1. Map of Brazil showing sampling sites for *Callinectes danae*. Brazilian states within the same region are represented with the same color. AP: Amapá; PA: Pará; RN: Rio Grande do Norte; PE: Pernambuco; AL: Alagoas; CE: Ceará; BA: Bahia; ES: Espírito Santo; RJ: Rio de Janeiro; SP: São Paulo; PR: Paraná; SC: Santa Catarina; RS: Rio Grande do Sul.

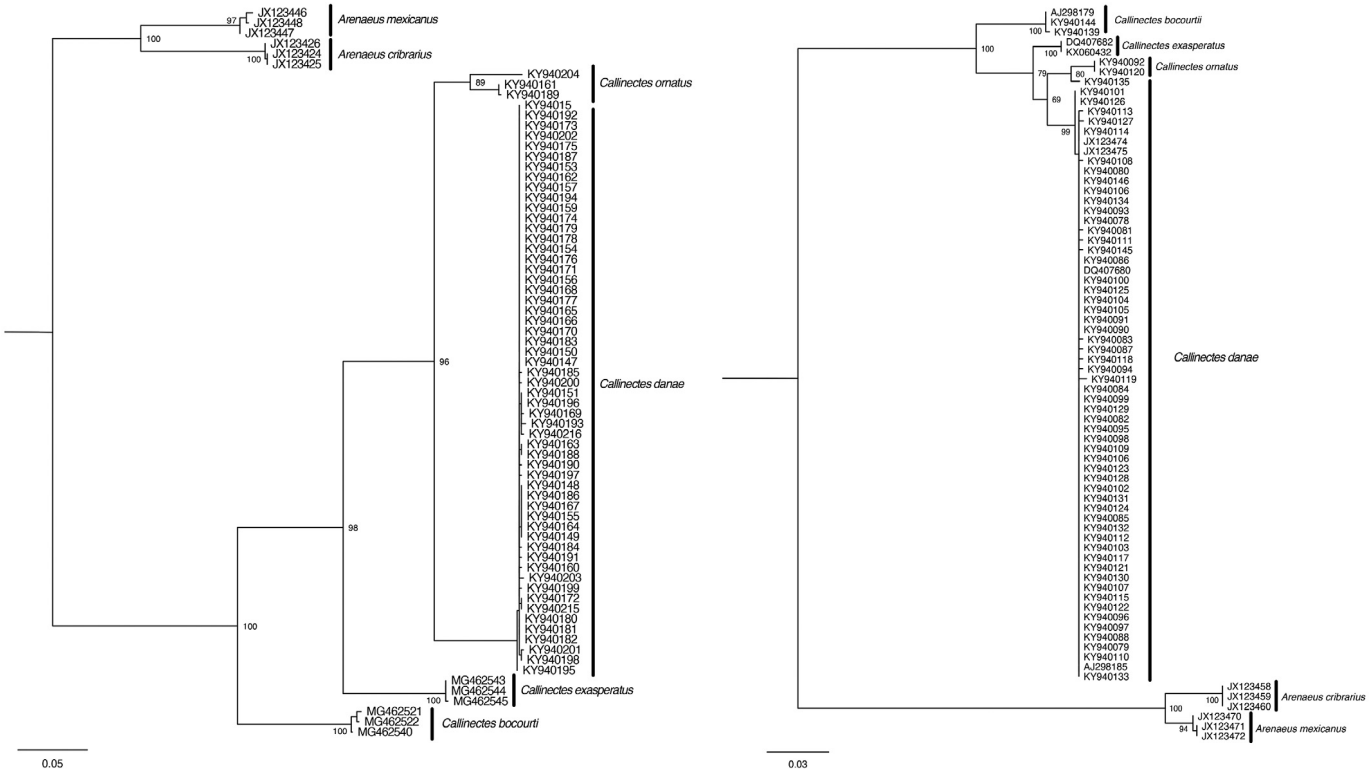

Fig. 2. Maximum-likelihood phylograms of *Callinectes danae* individuals. On the left: COI tree; On the right: 16S tree. Bootstrap values are indicated on nodes.

Table 1
Callinectes danae specimens from Brazil used for genetic analyses. GB: GenBank; CCDB: Coleção de Crustáceos do Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto (FFCLRP) – Universidade de São Paulo (USP); LCD/CCCD: Coleção Científica de Crustáceos Decápodes do Laboratório de Crustáceos Decápodes, Programa de Pós-Graduação em Aquicultura, Instituto de Oceanografia – Universidade Federal do Rio Grande (FURG); MZUSP: Museu de Zoologia – Universidade de São Paulo (USP).

Brazilian region	State	Locality	Voucher collection	GB numbers 16S	GB numbers COI
North	Amapá (AP)	Calçoene	CCDB 6112	KY940145	KY940215
	Pará (PA)	Salinópolis	LCD/CCCD 2024	KY940123	KY940192
	Pará (PA)	Salinópolis	LCD/CCCD 2024	KY940124	KY940193
	Pará (PA)	Belém	LCD/CCCD sn	KY940125	KY940194
	Pará (PA)	Belém	LCD/CCCD sn	KY940126	KY940195
Northeast	Ceará (CE)	Beberibe	CCDB 2339	KY940088	KY940157
	Ceará (CE)	Fortaleza	LCD/CCCD 02023	KY940121	KY940190
	Ceará (CE)	Fortaleza	LCD/CCCD 02023	KY940122	KY940191
	Rio Grande do Norte (RN)	Parnamirim	CCDB 3387	KY940090	KY940159
	Rio Grande do Norte (RN)	Parnamirim	CCDB 3387	KY940091	KY940160
	Alagoas (AL)	Maceió	MZUSP 6626	KY940111	KY940180
	Pernambuco (PE)	Ipojuca	CCDB 4508	KY940104	KY940173
	Pernambuco (PE)	Recife	LCD/CCCD 02965	KY940116	KY940185
	Pernambuco (PE)	Recife	LCD/CCCD 02965	KY940117	KY940186
	Pernambuco (PE)	Recife	LCD/CCCD 02965	KY940118	KY940187
	Pernambuco (PE)	Recife	LCD/CCCD 02965	KY940119	KY940188
	Pernambuco (PE)	Ipojuca	CCDB 4508	KY940103	KY940172
	Bahia (BA)	Entre Rios	CCDB 289	KY940086	KY940155
	Bahia (BA)	Porto Seguro	CCDB 1446	KY940087	KY940156
	Bahia (BA)	Salvador	LCD/CCCD 02019	KY940112	KY940181
	Bahia (BA)	Salvador	LCD/CCCD 02019	KY940113	KY940182
	Bahia (BA)	Salvador	LCD/CCCD 02019	KY940114	KY940183
	Bahia (BA)	Salvador	LCD/CCCD 02019	KY940115	KY940184
Southeast	Espírito Santo (ES)	Praia de Peruá	CCDB 4000	KY940098	KY940167
	Espírito Santo (ES)	Praia de Peruá	CCDB 4000	KY940099	KY940168
	Espírito Santo (ES)	Praia de Peruá	CCDB 4000	KY940100	KY940169
	Espírito Santo (ES)	Praia de Peruá	CCDB 4000	KY940101	KY940170
	Espírito Santo (ES)	Praia de Peruá	CCDB 4000	KY940102	KY940171
	Rio de Janeiro (RJ)	Ilha do Governador	LCD/CCCD 02964	KY940129	KY940198
	Rio de Janeiro (RJ)	Ilha do Governador	LCD/CCCD 02964	KY940130	KY940199
	Rio de Janeiro (RJ)	Ilha do Governador	LCD/CCCD 02964	KY940131	KY940200
	Rio de Janeiro (RJ)	Ilha do Governador	LCD/CCCD 02964	KY940132	KY940201
	Rio de Janeiro (RJ)	Ilha do Governador	LCD/CCCD 02964	KY940133	KY940202
	São Paulo (SP)	Ubatuba	CCDB 3445	KY940078	KY940147
	São Paulo (SP)	Ubatuba	CCDB 3445	KY940079	KY940148
	São Paulo (SP)	Ubatuba	CCDB 3445	KY940080	KY940149
	São Paulo (SP)	Ubatuba	CCDB 3445	KY940146	KY940216
	São Paulo (SP)	Cananéia	CCDB 3244	KY940081	KY940150
	São Paulo (SP)	Cananéia	CCDB 3244	KY940082	KY940151
	São Paulo (SP)	Cananéia	CCDB 3244	KY940083	KY940152
	São Paulo (SP)	Cananéia	CCDB 3244	KY940084	KY940153
	São Paulo (SP)	Cananéia	CCDB 3244	KY940085	KY940154
	São Paulo (SP)	Ubatuba	ULLZ 4179	DQ407680	n/a
	São Paulo (SP)	Ubatuba	ULLZ 4179	AJ298185	n/a
	São Paulo (SP)	Ubatuba	CCDB 1766	JX123474	n/a
	São Paulo (SP)	Ubatuba	CCDB 3665	JX123475	n/a
South	Paraná (PR)	Pontal do Paraná	LCD/CCCD 02012	KY940105	KY940174
	Paraná (PR)	Pontal do Paraná	LCD/CCCD 02013	KY940106	KY940175
	Paraná (PR)	Pontal do Paraná	LCD/CCCD 02015	KY940107	KY940176
	Paraná (PR)	Pontal do Paraná	LCD/CCCD 02012	KY940108	KY940177
	Paraná (PR)	Pontal do Paraná	LCD/CCCD 02012	KY940109	KY940178
	Paraná (PR)	Pontal do Paraná	LCD/CCCD 02931	KY940110	KY940179
	Santa Catarina (SC)	Baía da Babitonga	LCD/CCCD 3128	KY940127	KY940196
	Santa Catarina (SC)	Baía da Babitonga	LCD/CCCD 3009	KY940128	KY940197
	Rio Grande do Sul (RS)	Rio Grande	CCDB 3930	KY940093	KY940162
	Rio Grande do Sul (RS)	Rio Grande	CCDB 3930	KY940094	KY940163
	Rio Grande do Sul (RS)	Rio Grande	CCDB 3930	KY940095	KY940164
	Rio Grande do Sul (RS)	Rio Grande	CCDB 3930	KY940096	KY940165
	Rio Grande do Sul (RS)	Rio Grande	CCDB 3930	KY940097	KY940166
	Rio Grande do Sul (RS)	Ilha dos Marinheiros	LCD/CCCD 1678	KY940134	KY940203

Genetic differentiation between fishery stocks were assessed by pairwise Fst-values using Arlequin 3.5 (Excoffier and Lischer, 2010). A global (i.e. considering each Brazilian state a fishery stock) and hierarchical (i.e. considering Brazilian regions: North – AP: Amapá; PA: Pará; Northeast – RN: Rio Grande do Norte; PE: Pernambuco; AL: Alagoas; CE: Ceará; BA: Bahia; Southeast – ES: Espírito Santo; RJ: Rio de Janeiro; SP: São Paulo; South – PR: Paraná; SC: Santa Catarina; RS: Rio Grande do Sul) Analyses of Molecular Variance (AMOVA) (Excoffier et al., 1992) were computed with Arlequin 3.5. Significance levels were based on 1000 non-parametric permutations. Genetic distances were computed using Kimura-2-parameter (K2P) in MEGA 7 (Kumar et al., 2016).

We constructed a phylogram using maximum likelihood approach in IQ-TREE (Nguyen et al., 2015) performed in the online

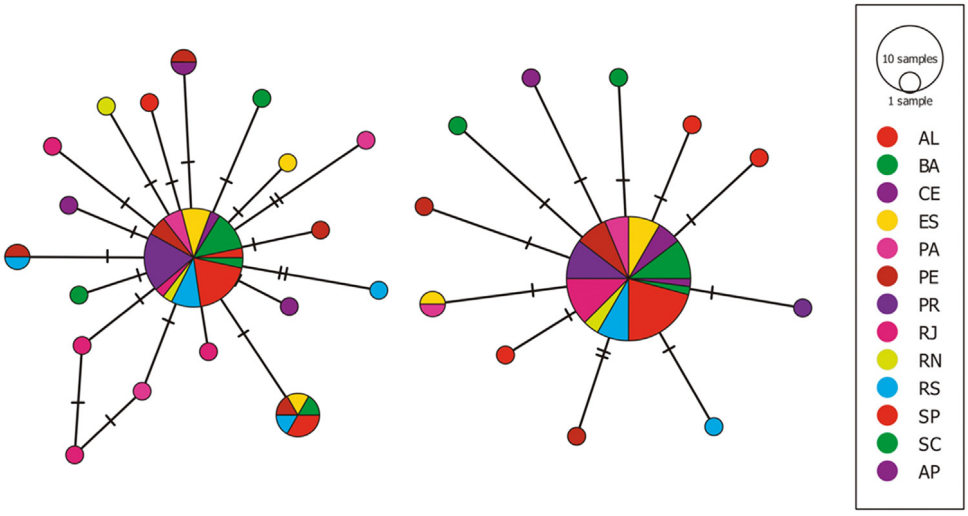

Fig. 3. Haplotype networks of *Callinectes danae*. On the left: COI (19 haplotypes). On the right: 16S (12 haplotypes). The size of the network circles is proportional to the haplotype frequency. AP: Amapá; PA: Pará; RN: Rio Grande do Norte; PE: Pernambuco; AL: Alagoas; CE: Ceará; BA: Bahia; ES: Espírito Santo; RJ: Rio de Janeiro; SP: São Paulo; PR: Paraná; SC: Santa Catarina; RS: Rio Grande do Sul.

platform Cyberinfrastructure for Phylogenetic Research (CIPRES) (Miller et al., 2010). We downloaded other *Callinectes* and Portunidae species sequences available from GenBank as outgroups (COI: *Arenaeus cribrarius* – JX123425, JX123426, JX123427; *Arenaeus mexicanus* – JX123446, JX123447, JX123448; *Callinectes ornatus* – KY940204, KY940161, KY940189; *Callinectes bocourti* – MG462521, MG462522, MG462540; *Callinectes exasperatus* – MG462543, MG462544, MG462545; 16S: *Arenaeus cribrarius* – JX123458, JX123459, JX123460; *Arenaeus mexicanus* – JX123470, JX23471, JX123472; *Callinectes ornatus* – KY940092, KY940120, KY940135; *Callinectes bocourti* – AJ298179, KY940139, KY940144; *Callinectes exasperatus* – DQ407682, KX060432). The evolutionary model that best fits our data was determined by IQ-TREE according to Bayesian Information Criterion (BIC) (Luo et al., 2010) and used for tree inference (best fit model COI: TPM2+F+G4; 16S: HKY+F+I). Branch support was assessed by ultrafast bootstrap with 1000 replicates. Haplotypes relationship was analyzed using a statistical parsimony network by means of the TCS program (Clement et al., 2000) as implemented in PopArt 1.7 (Leigh and Bryant, 2015).

3. Results

A total of 56 COI and 60 16S sequences were generated. We found 19 and 12 unique haplotypes for COI and 16S, respectively. Total nucleotide diversity was around 0.001 for both genes, ranging from 0–0.003 for COI and 0–0.002 for 16S. Total haplotype diversity was 0.362 (16S) and 0.687 (COI), ranging from 0–1. All the values are presented in Table 2.

Most of pairwise-FST values indicated lack of differentiation between populations (Table 3). The only significant results were between PR x RJ and SP x RJ. Likewise, AMOVA results for all tests showed more than 90% of genetic variation within populations suggesting lack of population genetic structure. Global Fst are 0.02 (COI) and 0.08 (16S), and 97% and 91% of variation is within populations, respectively. AMOVA Fst (among populations) and Fct (among groups) are extremely low and not significant in any case (Tables 4 and 5). Genetic distances are all below 0.3% indicating great similarity between populations as well (Table 6). Both phylograms present a high bootstrap value for *C. danae* and show no lineage splitting (Fig. 2). Likewise, both haplotype networks present a central haplotype shared by most crabs, characterizing a star-pattern shape, representing no genetic structure (Fig. 3).

Table 2
Genetic diversity values for each population of *Callinectes danae* (COI/16S). AP: Amapá; PA: Pará; RN: Rio Grande do Norte; PE: Pernambuco; AL: Alagoas; CE: Ceará; BA: Bahia; ES: Espírito Santo; RJ: Rio de Janeiro; SP: São Paulo; PR: Paraná; SC: Santa Catarina; RS: Rio Grande do Sul.

	n	Polymorphic sites	N haplotypes	Haplotypic diversity	Nucleotide diversity
AP	1/2	–/2	–/1	–/1	–/0.00183
PA	4/4	4/2	3/1	0.833/0.5	0.00304/0.0009
RN	2/2	1/1	2/0	1/0	0.00152/0
PE	6/6	4/3	5/3	0.933/0.6	0.00209/0.001
AL	1/1	–/–	–/–	–/–	–/–
CE	3/3	2/1	3/0	1/0	0.002/0
BA	6/6	2/2	3/1	0.6/0.33	0.00105/0.00068
ES	5/5	3/2	3/1	0.7/0.4	0.00182/0.0007
RJ	5/6	4/1	5/0	1/0	0.00277/0
SP	9/12	2/3	3/2	0.556/0.318	0.00096/0.00068
PR	6/6	0/2	1/1	0/0.33	0/0.0006
SC	2/2	1/2	2/1	1/1	0.00159/0.00226
RS	6/5	4/2	4/1	0.8/0.4	0.00203/0.0007
Total	56/60	19/12	19/12	0.687/0.362	0.00161/0.001

4. Discussion

Molecular markers have long been used to recognize distinct genetic stocks on fisheries resources (Waples et al., 2008 and references therein). Here, we demonstrated that the widespread swimming crab *Callinectes danae* represents a single species along its distribution across the Brazilian coast, and also that it can be considered a single genetic stock according to the markers used here. Our results, based on sampling *C. danae* individuals from all the Brazilian coastal regions, indicate we are dealing with only one species whose populations are not genetically differentiated, probably due its high dispersal potential (Shanks, 2009) and its wide ecological niche (Norse, 1978; Buchanan and Stoner, 1988; Leone et al., 2005; Andrade et al., 2015). These outcomes represent important information for fisheries management.

Many marine invertebrates present one or several pelagic larvae that might passively disperse via marine currents. For instance, the pelagic larval duration (PLD) may be a determinant factor for population connectivity since PLD is related with how far larvae can be transported (Shanks, 2009). The genera *Callinectes* usually present 8 zoea stages plus 1 megalopa, completing all its development in 50 days approximately (Costlow

Table 3
Pairwise-FST among populations of *Callinectes danae*. Below diagonal represents COI, upper diagonal represents 16S. Values in bold represent $p < 0.05$. AP: Amapá; PA: Pará; RN: Rio Grande do Norte; PE: Pernambuco; AL: Alagoas; CE: Ceará; BA: Bahia; ES: Espírito Santo; RJ: Rio de Janeiro; SP: São Paulo; PR: Paraná; SC: Santa Catarina; RS: Rio Grande do Sul.

COI/16S	*AP*	*PA*	*RN*	*PE*	*ES*	*CE*	*BA*	*AL*	*RJ*	*SC*	*PR*	*SP*	*RS*
AP	0	0.11111	0	0	0.17197	0.25	0.22581	0.33333	0.53846	0	0.22581	0.27897	0.17197
PA	0.14286	0	-0.2632	-0.0297	-0.281	-0.0909	0.01935	0.6	0.11111	0.11111	0.01935	0.03876	0.00641
RN	0.33333	-0.0602	0	-0.3044	-0.2903	0	-0.3044	1	0	0	-0.3044	-0.3266	-0.2903
PE	0	0.00557	-0.0534	0	-0.0154	-0.1539	0	0.33333	0	0	0	0.05167	-0.0154
ES	0.42857	0.01786	0.0411	-0.0751	0	-0.1321	0.00339	0.66667	0.04	0.17197	0.00339	0.01168	0
CE	0.2	-0.0059	-0.0313	0	0.0407	0	-0.1539	1	0	0.25	-0.1539	0.05167	-0.1321
BA	0.5	0.03836	0.08235	-0.0588	-0.097	0.06897	0	0.22581	0	0.22581	0	0	0.00339
AL	1	-1	-1	-1	-1	-1	-1	0	1	0.33333	0.71429	0.71429	0.66667
RJ	0.1	-0.0052	-0.0276	0.06587	0.07143	0.03729	0.09369	-0.8	0	0.53846	0	-0.0688	0.04
SC	0.33333	-0.0602	0	-0.0534	0.0411	-0.0313	0.08235	-1	-0.0276	0	0.22581	0.27897	0.17197
PR	1	0.11111	0.53846	0	0.04	0.25	0	0	**0.14286**	0.53846	0	0	0.00339
SP	0.54167	0.10027	0.14593	-0.0286	-0.0836	0.13314	-0.0759	-0.8333	**0.15516**	0.14593	0.02463	0	0.01168
RS	0.2	0.00557	-0.0534	-0.0909	-0.0751	0	-0.0588	-1	0.06587	-0.0534	0	-0.0286	0

and Bookhout, 1959; Bookhout and Costlow Jr., 1977; Dittel and Epifanio, 1984), indicating this as a probable condition of population connectivity.

Most of pairwise-Fst values falls under a threshold for little to moderate genetic differentiation, 0–0.15 (Wright, 1978). This emphasizes probable high connectivity among these populations. Values above this Fst threshold are those related to our least sampled populations, Amapá (AP) and Alagoas (AL) states. In these cases, one single haplotype was used in pairwise comparisons with more sampled populations, which can inflate interpopulation differentiation. On the other hand, we also show negative values, which occur because the algorithm considers population as finites and allows unbalanced comparisons (Weir and Cockerham, 1984). In this case, negative values represent more differentiation between individuals from the same populations than comparing with the other population (Holsinger and Weir, 2009) and can be considered as zero. Two pairwise comparisons (PR x RJ, SP x RJ) showed significant p-values for COI, but not for 16S. These results can be explained by the analysis detecting subtle differences due to the presence of singletons in RJ populations, while most of SP and PR individuals present the same haplotype. However, we also detected low divergence rates between these populations (0.2%). It is important to notice that there were no significant results between RJ and other populations, and higher divergence rates among other pairwise comparisons. AMOVA results also confirm the absence of genetic structure showing most of genetic variation within populations and no significant p-values. Likewise, the haplotype network stresses the probable high dispersion capability of the species by presenting a common haplotype shared by individuals from almost all localities (Tolley et al., 2005; Machado-Schiaffino and Garcia-Vazquez, 2011; Iacchei et al., 2014). All these results indicate lack of population genetic structure considering the markers used here. Even though minor differences were detected, we interpret this as not enough to characterize a different genetic stock.

Here, we also aimed to provide information for regional management, so we also analyzed our data considering the Brazilian regions. However, when we performed hierarchical analysis, there was not any sign of more than one stock across *C. danae* distribution on the Brazilian coast. Similarly, genetic divergence values are not higher than 0.3% considering both genes, even between Amapá (AP), northernmost population, and Rio Grande do Sul (RS), southernmost population. It is usually used a barcode gene (COI) threshold around 2% to separate crustacean species (Lefébure et al., 2006; da Silva et al., 2011), but *Callinectes* species gap can be 6%, and structured *Callinectes* populations can present up to 4% divergence under the same taxonomic entity (Peres and

Table 4
Analysis of molecular variance (AMOVA) testing for differences among populations and Brazilian regions using COI.

	Source of variation	Variance components	Fixation index	% variation
AMOVA Populations	Among populations	0.01035	0.02119	2.12
	Within populations	0.47817	–	97.88
AMOVA Regions	Among regions	−0.00187	−0.00383	−0.38
	Among populations within regions	0.01183	0.2040	2.42
	Within populations	0.47817	0.2413	97.96

Table 5
Analysis of molecular variance (AMOVA) testing for differences among populations and Brazilian regions using 16S.

	Source of variation	Variance components	Fixation Index	% variation
AMOVA Populations	Among populations	0.01885	0.08654	8.65
	Within populations	0.19894	–	91.35
AMOVA Regions	Among regions	−0.00573	−0.02645	−2.64
	Among populations within regions	0.02336	0.08143	10.79
	Within populations	0.19894	−0.02645	91.86

Mantelatto, 2020). Thus, populations of *C. danae* do not present any signs of limited dispersal. In agreement, the haplotype network shows individuals from different populations sharing the same haplotype reinforcing the idea of high connectivity (Liu et al., 2009; Sotelo et al., 2009; Rumisha et al., 2018).

Interestingly, a small-scale study on *C. danae* southern Brazilian populations showed genetic structure on some allozyme loci (Weber and Levy, 2000). One of the possible explanations to this contrasting result is the non-neutrality of allozymes (Parker et al., 1998; Schlötterer, 2004). This could lead to discrepancies between allozymes and mtDNA possibly due to the former being under positive or disruptive selection (Lenormand, 2002). Both types can cause similar patterns and result in population differentiation (Arnaud-Haond et al., 2003). This could represent that local conditions might be driving changes in alleles frequency in the populations analyzed by them. But we also have to consider that they found 2–7 migrants per generation. It is considered that one migrant per generation is enough to avoid genetic structure (Spieth, 1974). Combining our results and theirs, we can say that some specific allozyme loci are under some type of selection in these populations, but overall, populations are connected and may be considered as part of the same genetic stock.

Studies exploring the genetic variation of other economically important crabs along the Brazilian coast show a similar

Table 6
Kimura 2-Parameter genetic distance between populations. Below diagonal represents COI, upper diagonal represents 16S. Values are presented as percentage (%).

COI/16S	*AP*	*PA*	*RN*	*PE*	*AL*	*CE*	*BA*	*ES*	*RJ*	*SP*	*PR*	*SC*	*RS*
AP	0	0.2	0.1	0.2	0.3	0.1	0.2	0.2	0.1	0.2	0.2	0.2	0.2
PA	0.3	0	0.1	0.2	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1
RN	0.2	0.2	0	0.1	0.2	0	0	0	0	0	0.1	0.2	0
PE	0.2	0.2	0.2	0	0.3	0.1	0.2	0.2	0.1	0.2	0.2	0.1	0.2
AL	0.2	0.1	0.1	0.2	0	0.2	0.3	0.3	0.2	0.3	0.3	0.3	0.3
CE	0.3	0.2	0.2	0.2	0.1	0	0	0	0	0	0	0.1	0
BA	0.2	0.2	0.1	0.2	0.1	0.2	0	0.1	0	0.1	0.1	0.2	0.1
ES	0.2	0.2	0.1	0.2	0.1	0.2	0.1	0	0	0.1	0.1	0.2	0.1
RJ	0.3	0.3	0.2	0.3	0.2	0.3	0.2	0.2	0	0	0	0.1	0
SP	0.2	0.2	0.1	0.2	0.1	0.2	0.1	0.1	0.2	0	0.1	0.2	0.1
PR	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0	0.2	0.1
SC	0.2	0.2	0.2	0.2	0.1	0.2	0.1	0.1	0.2	0.1	0.1	0	0.2
RS	0.3	0.2	0.2	0.2	0.1	0.2	0.2	0.2	0.3	0.2	0.1	0.2	0

scenario. The highly consumed crabs *Ucides cordatus* (Linnaeus, 1763) and *Cardisoma guanhumi* Latreille, 1828 have been shown to present lack of differentiation among populations, despite high genetic diversity, when analyzed using mtDNA control region and COI (De Oliveira-Neto et al., 2007, 2008; Buranelli et al., 2019). Other important commercial swimming crab, *Callinectes sapidus*, also has presented lack of genetic structure among Brazilian populations at regional scales for mtDNA and microsatellite markers (Lacerda et al., 2016; Rodrigues et al., 2017). All these species present PLD above 40-days (Costlow and Bookhout, 1959; Rodrigues and Hebling, 1989), which may be responsible for constant migration among sites. Similarly, other *Callinectes* species from other regions also present lack of differentiation among their populations reinforcing the idea of causation between high larvae dispersion and genetic homogeneity (McMillen-Jackson and Bert, 2004; Cisneros-Mata et al., 2019).

However, there are some counter arguments regarding the relation between PLD and connectivity (Weersing and Toonen, 2009), but it is common to find support for this statement. For example, PLD and population differentiation seems to be the main factor affecting genetic variation of many marine invertebrates along Chilean coast (Haye et al., 2014). *Callinectes danae* occurs in high and low salinity waters, shallow waters and estuaries, indicating a wide ecological niche which could be favoring its lack of genetic structure (Norse, 1978; Buchanan and Stoner, 1988; Leone et al., 2005; Andrade et al., 2015). That is, putative barriers (e.g. Cabo Frio resurgence in southeastern Brazil) are not blocking the transport of larvae, and the capability of this species to habit different environments guarantees its establishment in new areas. Major marine currents such as the Brazil Current and North Brazil Current (Johns et al., 1998; Silveira et al., 2000), may be transporting *C. danae* larvae along the coast and promoting gene flow among populations (Palumbi, 2003). Additionally, ovigerous females can migrate offshore to release eggs, which can boost the chances of larvae transportation to further locations, even though adults are mainly located in estuaries (Branco and Masunari, 2000). Probably when there are no effective barriers, absence of physiological impediment for larval dispersion, and favorable conditions for adults settling in different regions, PLD guarantee continuous gene flow among populations, as observed among the coexistent mangrove crabs along western Atlantic (Buranelli and Mantelatto, 2019).

Considering our results and other examples presented, conservation and management could be designed considering the Brazilian coast as a single unit. Restocking strategies like rearing larvae in laboratory until adults and transferring them to possible depleted populations could be done regardless from where they were obtained. This would prevent, for example, collapse of populations due to exploitation and not affect the local genetic pool (Bell et al., 2008). Also, our results indicate that marine protected areas (MPA) could represent putative sources for replenish depleted areas. Unfortunately, MPA in Brazil are not set ideally, being more focused on coral reefs, and just 0.14% of the total coast is under no-take areas (Magris et al., 2013). Therefore, our results also indicate one of the conservation potentials of MPAs.

Genetic data is an important feature to take into consideration when dealing with a species conservation (IUCN, 2019). Identifying genetic stocks provides a baseline for conservation and management of these areas, which can prevent loss of intraspecific genetic diversity. The loss of genetic diversity represents harmful consequences for the biota such as inbreeding depression and loss of evolutionary potential (Frankham, 2005). Unfortunately, genetic data are still not commonly used in fisheries management and conservation plans. In the case of *C. danae* distributed in Brazil, our results confirmed that we are dealing with a single species along all the coast consisting of a single genetic stock. Furthermore, country-level management plans could be implemented since there are not distinct genetic stocks along its Brazilian distribution. Considering the mtDNA information (evolutionary timescale), we can affirm that *C. danae* in Brazil is not formed by separated genetic stocks and historical connectivity has been maintained. However, we must be aware that our data is based on mtDNA and fine-scale structure or recent population depletion might not have been detected (ecological timescale). We highly encourage the use of high-resolution molecular markers, such as single nucleotide polymorphisms (SNPs) or microsatellites, to have a better appraisal of current impacts of fisheries, fine-scale genetic structure, and local adaptation (Bernatchez et al., 2017). Future studies should combine genetic with population dynamics data to better understand the outcomes of fisheries activity.

CRediT authorship contribution statement

Pedro A. Peres: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization. **Mateus Lopes:** Conceptualization, Investigation, Writing - review & editing, Visualization. **Mariana Negri:** Investigation, Writing - review & editing. **Rafael Robles:** Investigation, Writing - review & editing. **Cleverson Rannieri Meira dos Santos:** Resources, Writing - review & editing. **Fernando L. Mantelatto:** Conceptualization, Methodology, Resources, Writing - original draft, Writing - review & editing, Visualization, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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