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Morphometric variations in the reef crab *Plagusia depressa* (Decapoda: Plagusiidae) in the Western tropical Atlantic

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ABSTRACT

Introduction: The reef crab *Plagusia depressa* is widely distributed in tropical oceans. In the Atlantic Ocean, this species is distributed in geographically distant regions with different environmental pressures, which may lead to morphological divergence.

Objectives: To explore morphometric differences in *Plagusia depressa* populations between coastal reefs and an oceanic island in the Western tropical Atlantic. Also, to examine the potential link between the species' phenotypic plasticity and environmental and geographic factors.

Methods: A total of 194 crabs were sampled from four Brazilian coastal and oceanic sites (Suape: n= 52, Tamandaré: n= 53, Barra Grande: n= 44, and Fernando de Noronha Archipelago: n= 45) from 2020 to 2022, under distinct anthropogenic and environmental influences. Linear and geometric morphometric analysis employed seven linear measurements and specific landmarks on the carapace, abdomen, and right chelae to pinpoint significant morphometric differences among these areas.

Results: The westernmost coastal population exhibited striking differences from the other regions. Male crabs in this population had a pronounced carapace rostrum, while females showed a narrower abdomen, longer telson, and chelae thinning and elongation. It is possible that the pronounced isolation in this area, along with patterns of changes in ocean currents, may influence our results. Female crab carapaces from the island area showed lateral enlargement and pronounced rostrum depressions. Furthermore, being farther from the mainland, this site has oceanic island environmental features, affecting the population through desiccation and air exposure. For male crabs, different right chelae shape across areas showed an impact of food capture and interaction with other organisms on their phenotypic plasticity.

Conclusion: Environmental factors such as tidal exposure and habitat composition might affect the phenotypic plasticity of tidal crabs. Moreover, a biogeographical barrier in Northeastern Brazil, which was hitherto given little consideration, holds important implications for the biogeography of the Western tropical Atlantic.

Key words: biogeography; environmental pressures; geometric morphometry; marine ecology; phenotypic plasticity.

RESUMEN

Variaciones morfométricas en el cangrejo de arrecife *Plagusia depressa* (Decapoda: Plagusiidae) en el Atlántico tropical occidental

Introducción: El cangrejo de arrecife *Plagusia depressa* se distribuye ampliamente en los océanos tropicales. En el océano Atlántico, esta especie se distribuye en regiones geográficamente distantes con diferentes presiones ambientales, lo que puede llevar a una divergencia morfológica.
Objetivos: Explorar las diferencias morfométricas en las poblaciones de *Plagusia depressa* entre arrecifes costeros y una isla oceánica en el Atlántico tropical occidental. Además, examinar el posible vínculo entre la plasticidad fenotípica de la especie y los factores ambientales y geográficos.
Métodos: Se muestrearon un total de 194 cangrejos en cuatro sitios costeros y oceánicos brasileños (Suape: n= 52, Tamandaré: n= 53, Barra Grande: n= 44 y Archipiélago Fernando de Noronha: n= 45) desde 2020 hasta 2022, bajo influencias antropogénicas y ambientales distintas. El análisis morfométrico lineal y geométrico empleó siete medidas lineales y puntos de referencia específicos en el caparazón, abdomen y quelas derechas para señalar diferencias morfométricas significativas entre estas áreas.
Resultados: La población costera más occidental mostró diferencias sorprendentes con las otras regiones. Los cangrejos machos en esta población presentaban un rostro de caparazón pronunciado, mientras que las hembras mostraban un abdomen más estrecho, telson más largo y adelgazamiento y alargamiento de las quelas. Es posible que el aislamiento pronunciado en esta área, junto con patrones de cambios en las corrientes oceánicas, puedan influir en nuestros resultados. Los caparazones de las cangrejas hembra de la zona de la isla mostraron un ensanchamiento lateral y depresiones de rostro pronunciadas. Además, al estar más lejos del continente, este sitio tiene características ambientales de isla oceánica, lo que afecta a la población a través de la desecación y la exposición al aire. Para los cangrejos machos, diferentes formas de quelas derechas en diferentes áreas indican un impacto de la captura de alimentos y la interacción con otros organismos en su plasticidad fenotípica.
Conclusión: Factores ambientales como la exposición a las mareas y la composición del hábitat podrían desempeñar un papel en la plasticidad fenotípica de los cangrejos de marea. Además, una barrera biogeográfica en el noreste de Brasil, que hasta ahora se había tenido en poca consideración, tiene importantes implicaciones para la biogeografía del Atlántico tropical occidental.

Palabras clave: biogeografía; presiones ambientales; morfometría geométrica; ecología marina; plasticidad fenotípica.

INTRODUCTION

Conspecific individuals can differ in several specific nuances, ranging from evident differences in traits, such as sex, color, and size, to less conspicuous properties, such as behavior, genetics, and subtle differences in body shape. Individual variations in morphology are a major focus of evolutionary biology since natural selection acts on them (Afkhami et al., 2016; Cadrin et al., 2014). Identifying and describing population variations and biogeographical barriers is essential to answer fundamental questions in evolutionary biology, as well as providing subsidies for the evaluation and management of fisheries through stock identification, habitat utilization, migration patterns and response to environmental changes (Cadrin et al., 2014; Hopkins & Thurman, 2010).

Brachyura crab studies have identified morphological divergences between populations, which may be influenced over time by environmental factors (phenotypic plasticity) due to distinct selective stresses when populations are geographically isolated (Teschima et al., 2016; Silva et al., 2010). In the oceans, larval dispersal promotes marine life and connectivity within and between populations, leading to the exchange of individuals among distant or geographically isolated populations. This connectivity carries significant implications for the evolution and ecology of the species (Becker et al., 2007).

Ocean currents significantly influence marine environments, particularly impacting the movements and dispersal of planktonic larval species (Chapman et al., 2011). In the Tropical Western Atlantic (TWA), various current systems, including the central branch of the South Equatorial Current (cSEC), the Brazil Current (BC), and the North Brazil Undercurrent (NBUC), play vital functions (Fig. 1) (Dossa et al., 2021). TWA and the Brazilian coast areas feature two well-defined biogeographic barriers: the low-salinity Amazon River plume and the cold-water upwelling of Cabo Frio (Floeter et al., 2008; Rocha, 2003; Tosetto et al., 2022). Another potential barrier that is less evident and unexplored, is the cape of Ponta do Calcanhar (Fig. 1). Many studies have shown that this geographical point tends to substantially restrict gene exchange between populations to the North and South of this cape, acting as a biogeographical barrier for species with planktonic larval stages, probably due to the lack of any advective transport in a southerly direction at this cape (e.g. Hampton et al., 2014; Melo et al., 2020; Shanks, 2009; Weersing & Toonen, 2009). Studies on the connectivity of brachyuran crabs have reported patterns of intraspecific morphological variation between populations to the North and South of Ponta do Calcanhar, as observed in populations of the genus *Uca* (Hampton et al., 2014; Wieman et al., 2014) and in semi-terrestrial crab *Armases angustipes* (Rathbun, 1897) (Marochi et al., 2017), indicating that such geographical features and environmental

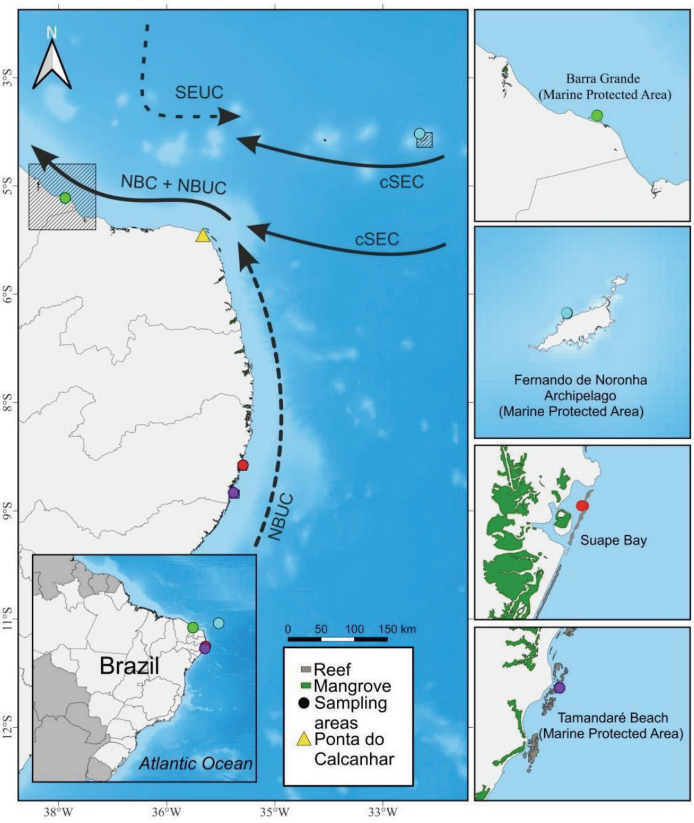

Fig. 1. The study areas in the Western Tropical Atlantic, where *Plagusia depressa* specimens were captured. Barra Grande Marine Protected Area, Suape Bay, Port and Industrial Area, Tamandaré Beach Marine Protected Area and Fernando de Noronha Archipelago Marine Protected Area. Yellow Triangle: Ponta do Calcanhar Cape, a potentially relevant biogeographic barrier (for details, see text). Ocean currents shown in the map, according to (Dossa et al., 2021): North Brazil Undercurrent (NBUC), North Brazil Current (NBC), the central branch of the South Equatorial Current (cSEC), South Equatorial Undercurrent (SEUC).

pressures may influence phenotypic plasticity within populations.

A key characteristic of the Tropical Western Atlantic (TWA) off Northeastern Brazil is the presence of oceanic islands, as Fernando de Noronha Archipelago. This insular environment is separated by kilometers of distance, and may support species with limited recruits, necessitating their management as distinct ecological populations (Palumbi, 2003; Teschima et al., 2016). The average dispersal range for fish and invertebrate larvae is 25 to 150 km (Palumbi, 2003), while Brazilian oceanic islands are over 300 km from the coast, leading to reduced gene flow among populations, implying in the demographic rates and population dynamics of the species and that can affect their survival, reproduction, and overall population health. This isolation has been shown to result in intraspecific variations in certain marine invertebrates, including the sally lightfoot crabs *Grapsus grapsus* (Linnaeus, 1758) and *Grapsus adscensionis* (Osbeck, 1765) (Freire et al., 2021; Teschima et al., 2016) and the chaetognath *Flaccisagitta enflata* (Grassi, 1881) (Melo et al., 2020).

The reef crab *Plagusia depressa* (Fabricius, 1775) (Brachyura: Plagusiidae) is widely distributed in the tropical oceans and in the Western Atlantic, *P. depressa* occurs on Brazil's Northeast coast and oceanic islands Fernando de Noronha, São Pedro and São Paulo Archipelago, Rocas Atoll, and Trindade and Martin Vaz Archipelago (Coelho et al., 2008; Melo, 1996; Oliveira-Almeida & Lopes-Carvalho, 2014). This species can be found in crevices of shallow subtidal rocks and the intertidal zones of coral reefs (Coelho et al., 2008), in general, on the reef line furthest from the shore. This species is commercially exploited and consumed by local populations, particularly in some Brazilian coastal areas (Freitas & Santos, 2007). Despite its wide distribution, studies on *P. depressa* in the Western Atlantic is limited, focusing mainly on body growth and mortality (Coelho et al., 2004), population structure (de Oliveira-Rocha et al., 2019; Freitas & Santos, 2007; Oliveira-Rocha & Paiva-Guimarães, 2016), gonadal development (Paiva-Guimarães et al., 2021), and feeding habits (de Lemos et al., 2019). Challenges in studying this species arise from its cryptic nocturnal behavior and difficulty in capturing within reef crevices, contributing to the lack of greater contributions to assessments of its ecology and formal quantitative stocking efforts.

Understanding the biological and ecological characteristics of this species across its distribution range -such as population dynamics, interpopulation connectivity, and the impacts and pressures on its habitat- is crucial for a deeper comprehension of these populations and for the formulation of effective strategies for the conservation and management of this species. Thus, the objective of this study was to investigate the potential existence of variation patterns in the shape and size of *P. depressa* populations at three coastal sites and one oceanic island in the WTA, each with varying conservation statuses and environmental characteristics, using two different morphometric techniques (linear and geometric). We tested the hypothesis that *P. depressa* demonstrates phenotypic plasticity across populations based on environmental and geographical factors.

MATERIAL AND METHODS

Sexually mature specimens of *P. depressa* (i.e. specimens with carapace widths larger than 24 mm for males and 27 mm for females, according to de Oliveira-Rocha et al. (2019) were collected in three coastal zones and one oceanic insular ecosystem with different levels of protection: Barra Grande Marine Protected Area (BG); Tamandaré beach (TM) within Costa dos Corais Marine Protected Area (MPA); Suape Beach (SB) with open, unrestricted access for tourism and fisheries, and in the oceanic Fernando de Noronha Archipelago (FN) marine protected area (Table 1, Fig. 1). Among these areas, the SB port and industrial area has the lowest level of protection, and reef crab meat is regularly offered and sold there (known as "aratú-da pedra"). At BG and TM marine protected areas, the capture

Table 1
Sampling areas for the reef crabs *Plagusia depressa*, with area characterization and sampling period.

Sampling area	Coordinates	Area characterization	Sampling period
Fernando de Noronha Archipelago (FN)	3º15’ S & 36º10’ W	MPA, insular area, crustacean harvest and fishing activities prohibited by federal laws, and strong tourism activity (Teixeira, 2003)	2020, Nov
Barra Grande (BG)	4°40’04” S & 37°24’54” W	MPA, urban, sustainable crustacean fishing activity (de Andrade-Meireles et al., 2017)	2022, Jan
Suape Bay (SB)	8º22’ S & 34º56’W	Industrial and port complex, intensive fishing activities, industrial effluents and domestic sewage (Lima-Barcellos et al., 2018)	2021, Nov
Tamandaré Beach (TM)	8º45’ S & 35º08’ W	MPA, urban, sustainable fishing and tourism activities, agriculture activities (Maida & Ferreira, 2003)	2020, Dec

MPA: Marine Protected Area.

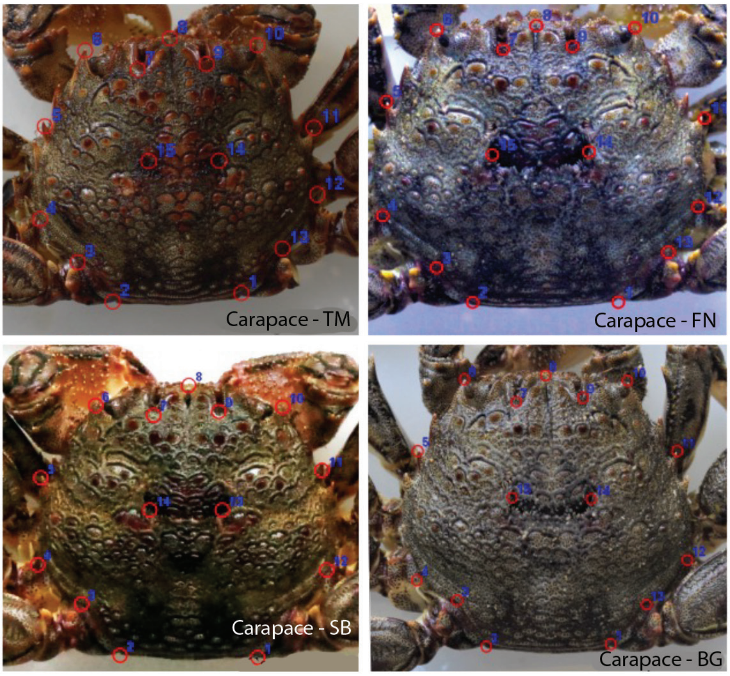

Fig. 2. Carapaces of *Plagusia depressa* specimens from sampled areas photo-documented in TPSDig software (v. 2.31) with their respective landmarks for geometric morphometric analysis. TM: Tamandare Beach; FN: Fernando de Noronha Archipelago; SB: Suape Bay; BG: Barra Grande.

of reef crabs is permitted for subsistence, but there is no regular commercial activity based on this species. On the oceanic FN island, the capture of this species is strictly forbidden and effectively enforced.

Structure measurements and anatomical landmarks: All individuals were identified, sexed, weighed, and measured. Body measures were obtained using precision calipers (nearest 0.01 mm). The measures were: A: carapace length (CL), B: carapace width (CW), C: abdomen length (AL); D: abdominal width (AW); E: right chelae length (RCL) F: right chelae width (RCW) (Fig. 2, Fig. 3, Fig. 4, Fig. 5).

Morphological variation in body shapes was assessed using geometric morphometric methods (Teschima et al., 2016; Thurman et al., 2021; Zelditch et al., 2012). Images were taken with the aid of a tripod attached to a camera (Canon EOS Model T3i) that was maintained parallel to the plane, for standardization. To each crab from the sampled locations, three pictures were photo-documented: dorsal, ventral, and right chelae (Fig. 2, Fig. 3, Fig. 4) Landmarks were distributed to better obtain the shape of the animal using the TPSDig software (version 2.31, Rohlf, 2010) based on previous studies using other brachyuran crabs (e.g. Marochi et al., 2017; Teschima et al., 2016; Thurman et al., 2021; Silva et al., 2010). For the carapace, 15 anatomical landmarks were distributed: being 11 landmarks for female abdomens, 10 landmarks for male abdomens, and six landmarks for right chelae (Fig. 5).

Morphometric Analysis: The degree of morphologic divergence among the studied populations of *P. depressa* was assessed using two complementary methods: linear and geometric morphometric analyses (LMA and GMA, respectively). First, we analyzed the influence of linear measurements on the morphometric variation of the different sampling areas. For this purpose, a Principal Component Analysis (PCA) was conducted to describe, graphically, which body structures most influenced the separation between the sampling areas. Next, to identify possible morphological divergences through the shape of the body structures in the studied populations, a geometric morphometric analysis (GMA) was adopted. For this, a Generalized Procrustes Analysis (GPA) was conducted with raw landmark coordinates within superimposed configurations, based on the centroid (i.e. mass center of the configuration). GPA overlapping removed the effect of position, orientation, and size of landmark configuration, in such a way that the aligned configurations corresponded exclusively to shape changes (Adams et al., 2004).

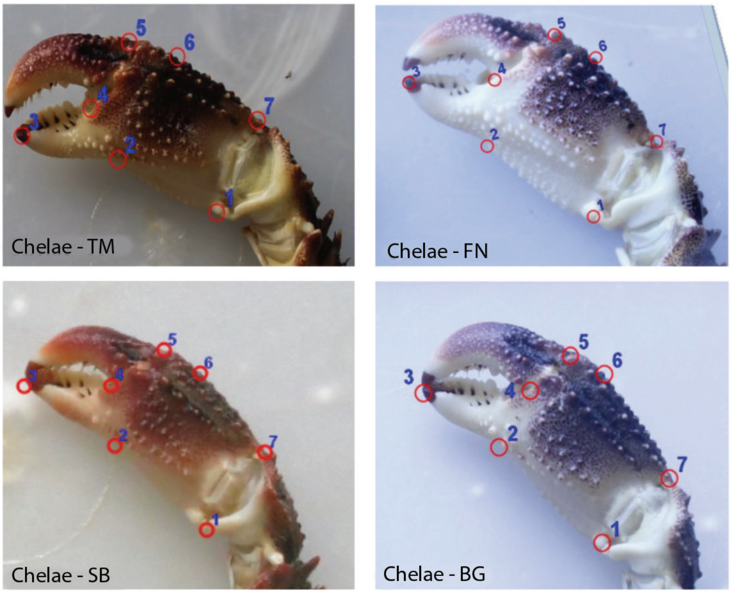

Fig. 3. Chelae of *Plagusia depressa* specimens from sampled areas photo-documented in TPSDig software (v. 2.31) with their respective landmarks for geometric morphometric analysis. TM: Tamandare Beach; FN: Fernando de Noronha Archipelago; SB: Suape Bay; BG: Barra Grande.

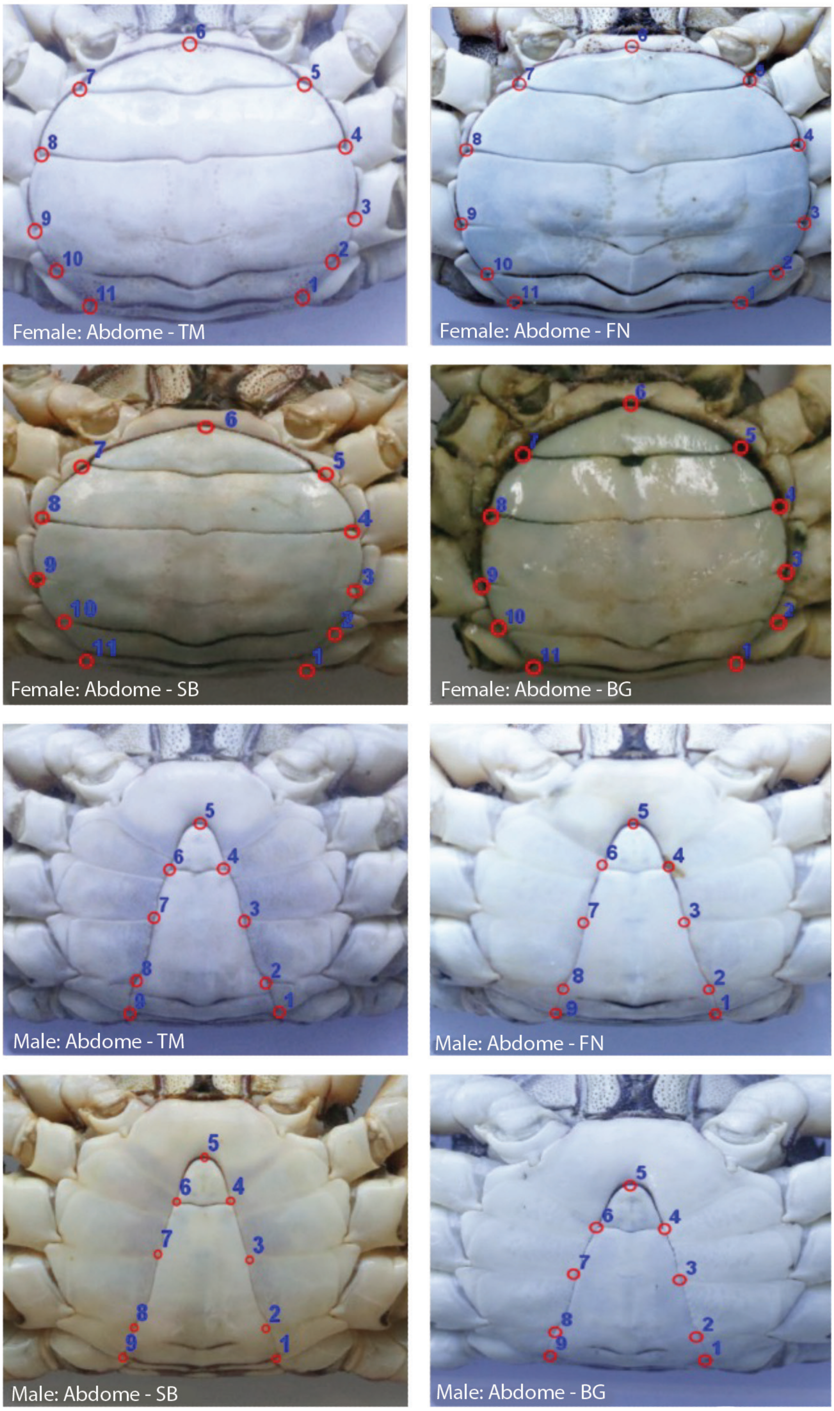

Fig. 4. Abdomen of *Plagusia depressa* male and female specimens from sampled areas photo-documented in TPSDig software (v. 2.31) with their respective landmarks for geometric morphometric analysis. TM: Tamandare Beach; FN: Fernando de Noronha Archipelago; SB: Suape Bay; BG: Barra Grande.

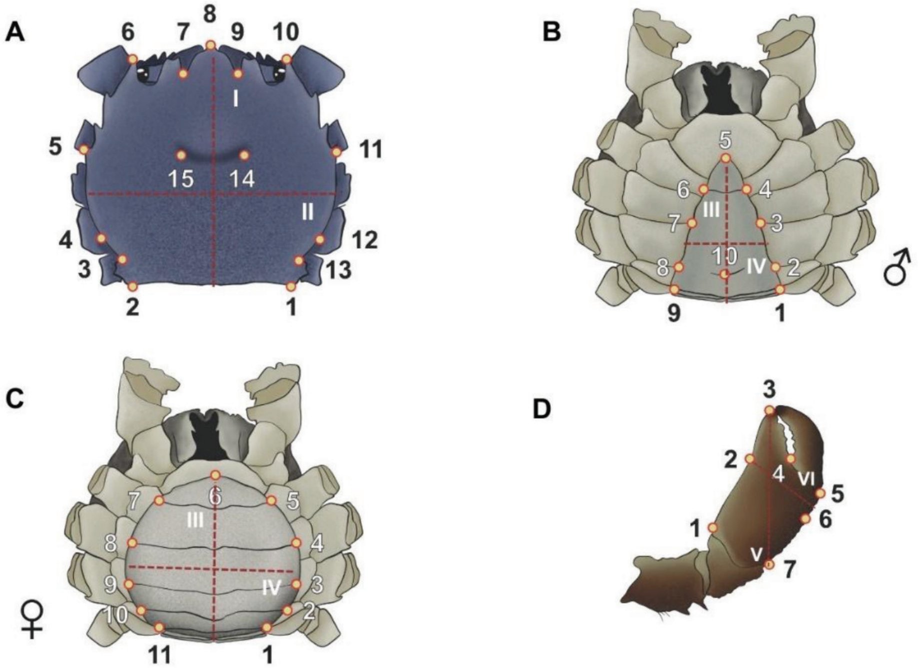

Fig. 5. Structure measurements and anatomic landmarks for *Plagusia depressa* specimens used for linear and geometric morphometric analysis. **A.** Carapace: 1 and 2: posterior margins; 3 and 13: concavity limits of the fifth pereiopods; 4 and 12: convex points of the posterior lateral region; 5 and 11: spines of maximum carapace width; 6 and 10: anterolateral spine tips; 7, 8 and 9: rostrum dent depressions; 14 and 15: distal points of the cardiac line structure; dotted lines: I: carapace length; II: carapace width. **B.** Male abdomen: 1 and 9: abdomen anterior margin; 2 and 8: third abdominal somite posterolateral margins; 3 and 7: fourth abdominal somite lateral margins; 4 and 6: fifth abdominal somite anterolateral margins; 5: top of the telson; 10: midpoint of the third abdominal somite; dotted lines: III: abdomen length; IV: abdomen width. **C.** Female abdomen: 1 and 11: abdomen anterior margin; 2 and 10: third abdominal somite posterolateral margin; 3 and 9: fourth abdominal somite lateral margin; 4 and 8: fifth abdominal somite anterolateral margin; 5 and 7: sixth abdominal somite anterolateral margin; 6: telson tip. **D.** Right chelae: 1 and 7: lower and upper attachment point of carpus with manus; 2: maximum concave point of the lower manus region; 3: polex tip; 4: lower point of dactylar joint with manus; 5: upper point of dactylar joint with manus; 6: maximum convex point of the upper manus region; dotted lines: V: chelae length; VI: chelae width.

Similarly to LMA, a Principal Component Analysis (PCA) was conducted to identify the main characteristics of the shapes. Then, Canonical Variance Analysis (CVA) was performed, with 10 000 permutations, to find the shape characteristics that best distinguish and separate the sampling areas, using Procrustes' Distance (Proc. Dist.). Differences between the forms were tested by applying the Hotelling test (T^2) with Bonferroni correction in Discriminant Analysis (DA). Thin-plate spline functions (Klingenberg, 2011) were generated between the groups that presented significant differences in DA using the MorphoJ 2.0 software. In all instances, the level of statistical significance was set at $p \leq 0.05$ for rejecting the null hypothesis.

A multivariate regression analysis was carried out to determine the influence of size on shape (allometry) in the dataset using centroid size (size variable) as an independent variable and shape (Procrustes coordinates) as a dependent variable (Klingenberg, 2016) with p-values estimated by permutation tests (10 000 interactions). This test simulates the null hypothesis of complete independence between size and shape by randomly reassigning the sizes and shapes to each other, indicating percent allometry (%) between shape and size in the population studied.

RESULTS

A total of 194 *P. depressa* specimens (87 females and 107 males) were collected: 44 at Barra Grande (BG), 52 in Suape Bay (SB), 53 at Tamandaré Beach (TM), and 45 at Fernando de Noronha Archipelago (FN). Adult crabs varied considerably in carapace width for both females and males (Table 2).

Table 2
Populations of reef crab *Plagusia depressa* used for morphometric analyses.

Sampling Area	Sex	N	CW	Mean (St. Dev.) CW
BG	F	17	31-54 mm	36 mm (± 8.2)
	M	27	24-57 mm	46 mm (± 10.9)
SB	F	25	32-51.5 mm	39 mm (± 4.1)
	M	27	32.5-44 mm	38 mm (± 3.0)
TM	F	26	33.5-52 mm	42.5 mm (± 5.1)
	M	27	33.5-52 mm	44 mm (± 5.5)
FN	F	19	27-49.5 mm	34 mm (± 5.3)
	M	26	26.5-54 mm	36 mm (± 7.0)

Sample size (N), Carapace width (CW), with their respective mean and standard deviation (St. Dev). Sampling areas: Barra Grande (BG), Suape Bay (SB), Tamandaré Beach (TM), Fernando de Noronha Archipelago (FN).

In the Principal Component Analysis (PCA) conducted within the linear morphometric analysis for males (PCA, Fig. 6), the variable RCL contributed the most to differences between Tamandaré (TM) and Suape Bay (SB) (Fig. 7). These PCA results explained 92 % of the variation in the first two components. PC1 explained 87.4 %, with a strong influence of right chelae length (RCL).

In females, PCA, showed that there were strong influences of the right chelae width (RCW), abdomen width (AW), and carapace height (CH) on the separation between areas (Fig. 7). These structures indicated that these variables were important in the separation of females of the Fernando de Noronha Archipelago (FN) population from the other areas. The first two components explained 86.7 % of the variability, being 74.2 % explained by PC1 and 12.5 % by PC2.

According to the results of the geometric morphometric analysis (GMA), the vectors

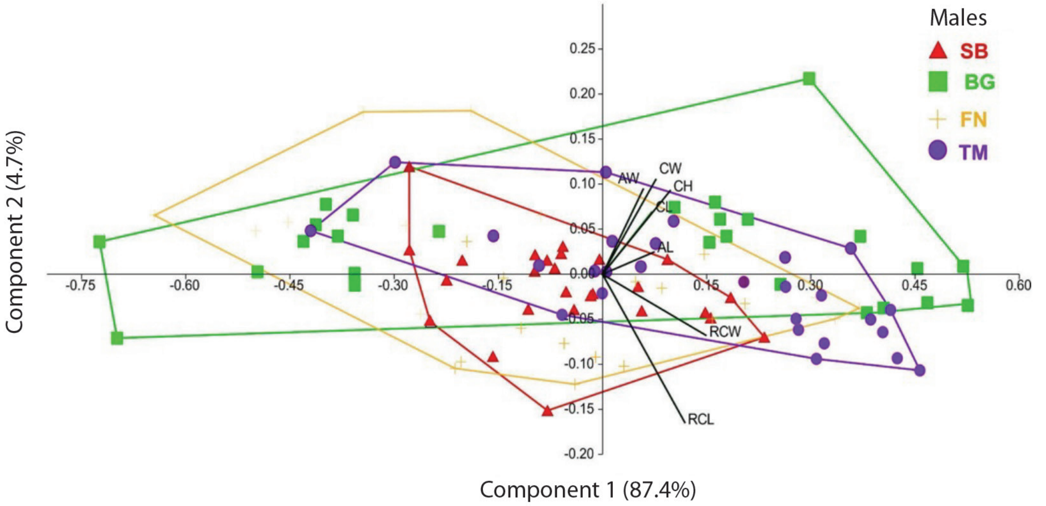

Fig. 6. Principal Component Analysis (PCA) of male *Plagusia depressa* populations of the variables studied in the areas studied. Carapace width (CW); carapace length (CL) carapace height (CH); abdomen width (AW); abdomen length (AL); right chelae width (RCW); right chelae length (RCL).

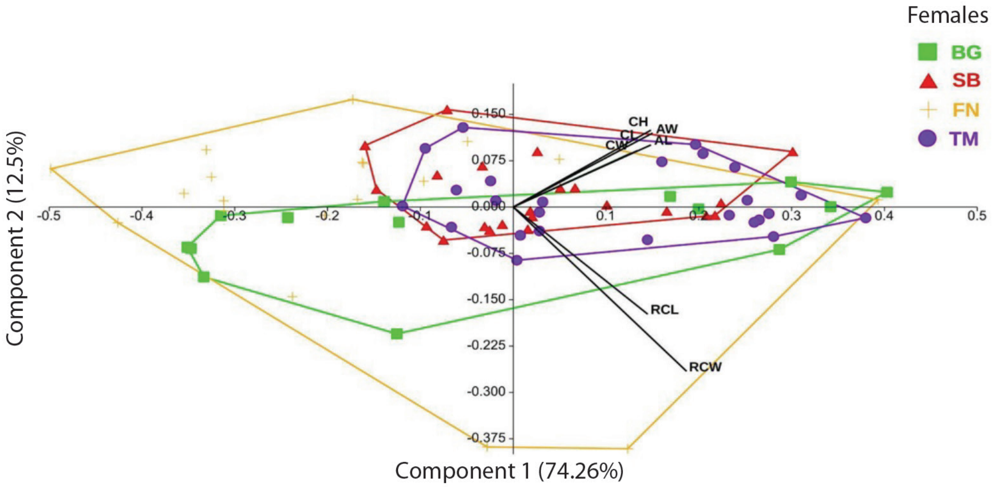

Fig. 7. Principal Component Analysis (PCA) of female *Plagusia depressa* populations of the variables studied in the areas studied. Carapace width (CW); carapace length (CL) carapace height (CH); abdomen width (AW); abdomen length (AL); right chelae width (RCW); right chelae length (RCL).

below can be interpreted and visualized as a shape change per unit of size change. Females and males of *P. depressa* showed low allometric percentages with values less than 12 % in all multivariate regressions analyzed, indicating that the effect of structure sizes has little influence on the morphological variation in reef crab population in studied areas. The carapace and abdomen of females showed 6.41 % and 11.16 % of allometric percentage, respectively, with highly significant permutation values (Multivariate regression; $p < 0.0001$). For chelae, the allometric value was about 1 % and there was no significant difference between shape and centroid size in females ($p = 0.57$, Fig. 8).

Conversely, male crabs exhibited values of 11.1 % of allometric percentage in carapace and chelae multivariate regression and 3.5 % for male abdomen, with significant permutation values in all sampled reef environments (Multivariate regression, $p < 0.0001$).

Carapace shapes: *P. depressa* populations exhibited significant differences in carapace shapes between populations. Procrustes distance values of males were different between Tamandaré (TM) and Barra Grande (BG) populations (CVA; $p < 0.05$, Table 3). The CVA results explained 86 % of the morphological variations between the studied areas (Fig. 9A). Males from TM presented a more concave fourth pereiopod region (3 and 13 points) than the male population from BG and a narrowing of the cardiac lines (14 and 15 points). On the other hand, the BG population presented the region corresponding to the rostrum more pronounced than TM. According to the discriminant analysis (DA) through cross-validation between the groups analyzed, the percentage of correct allocation of the BG-TM male populations was 85 and 73 %, respectively ($p < 0.0001$) (Fig. 6B).

In the same way as the linear results, the shape data of the female crabs of *P. depressa* for the FN population were different from the other areas (CVA, $p < 0.05$, Table 3) with CVA results explaining 88 % of the first two variables (Fig. 6C). The FN female population showed enlargement in the posterior lateral region (4 and 12 points) and more pronounced rostrum depressions (7 and 9 points) in relation to the coastal areas studied. According to the discriminant analysis through cross-validation between the analyzed groups, it was possible to

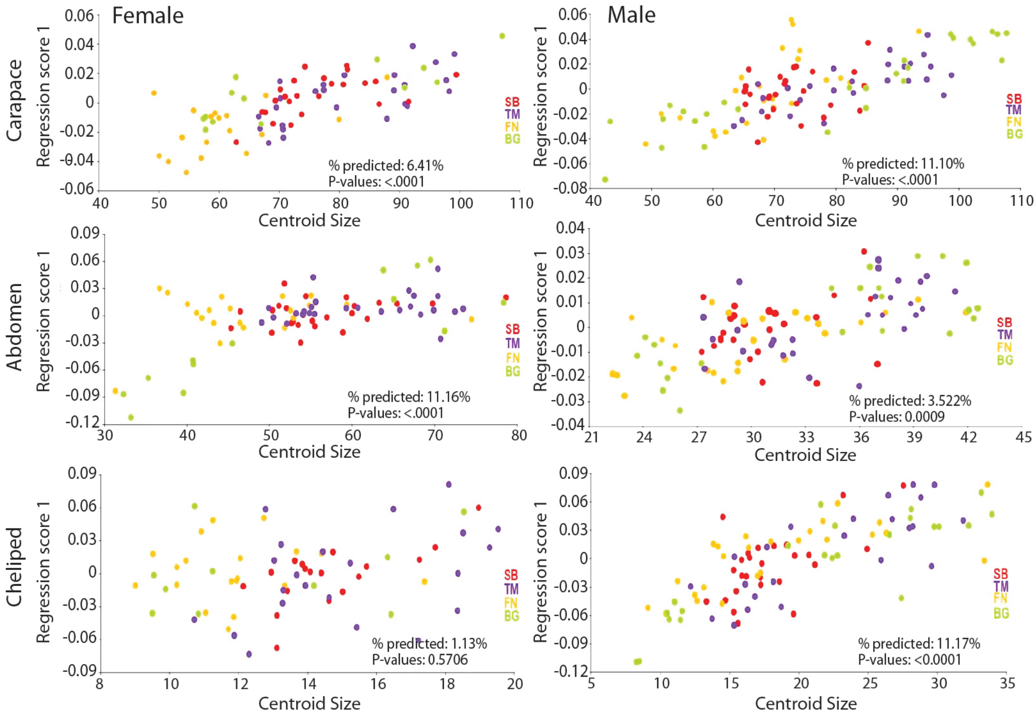

Fig. 8. Multivariate regression of influence of size on shape (allometry) in *Plagusia depressa* populations. Centroid size (independent variable) and regression score-Procrustes distance (dependent variable). Barra Grande-BG. Suape Bay-SB. Tamandaré Beach-TM and Fernando de Noronha Archipelago-FN. % prediction: allometric percentage with corresponding p-values corrected from permutation tests (10 000 permutation rounds).

Table 3

Procrustes distance and corresponding "p"-values referring to the pairwise structure shapes differences between the male and female of *Plagusia depressa* populations.

BG x SB		Procrustes Distance/ P-values					
		BG x TM	BG x FN	SB x TM	SB x FN	FN x TM	
MALE	Carapace	0.015/p = 0.326	0.023/**p = 0.008**	0.022/p = 0 .083	0.016/p = 0.053	0.017/p = 0.157	0.018/p = 0.194
	Abdomen	0.026/**p < 0.001**	0.083/**p < 0.001**	0.020/**p = 0.021**	0.035/**p < 0.001**	0.031/**p < 0.001**	0.013/p = 0.123
	Chelae	0.082/ **p < 0.001**	0.050/**p < 0.001**	0.046/**p = 0.003**	0.046/**p < 0.001**	0.055/**p < 0.001**	0.037/**p = 0.034**
FEMALE	Carapace	0.015/p = 0.464	0.023/p = 0.061	0.003/**p = 0.001**	0.016/p = 0.464	0.026/**p < 0.001**	0.027/**p < 0.001**
	Abdomen	0.033/**p = 0.017**	0.036/**p < 0.001**	0,031/p = 0.057	0.015/p = 0.145	0.015/p = 0.170	0.015/p = 0.128
	Chelae	0.054/**p = 0.014**	0.042/p = 0.173	0.057/**p = 0.012**	0.033/p = 0.136	0.019/p = 0.730	0.038/p = 0.077

Barra Grande-BG. Suape Bay-SB. Tamandaré Beach-TM and Fernando de Noronha Archipelago-FN. The P-values were corrected from permutation tests (10 000 permutation rounds) for Procrustes distances among groups.

observe that the percentage of correct allocation of females in the Fernando de Noronha Archipelago was higher than 61 % in relation to the other areas (Fig. 9D).

Abdomen shapes: Abdomen shapes also showed distinct variations in patterns in both male and female *P. depressa* populations from the WTA. Male crab populations showed significant differences between all areas (p < 0.05, Table 3) except between FN and TM (p = 0.123, Table 3). In general, males from SB showed a narrowing of the posterior lateral region at the margin of the third abdominal somite (2 and

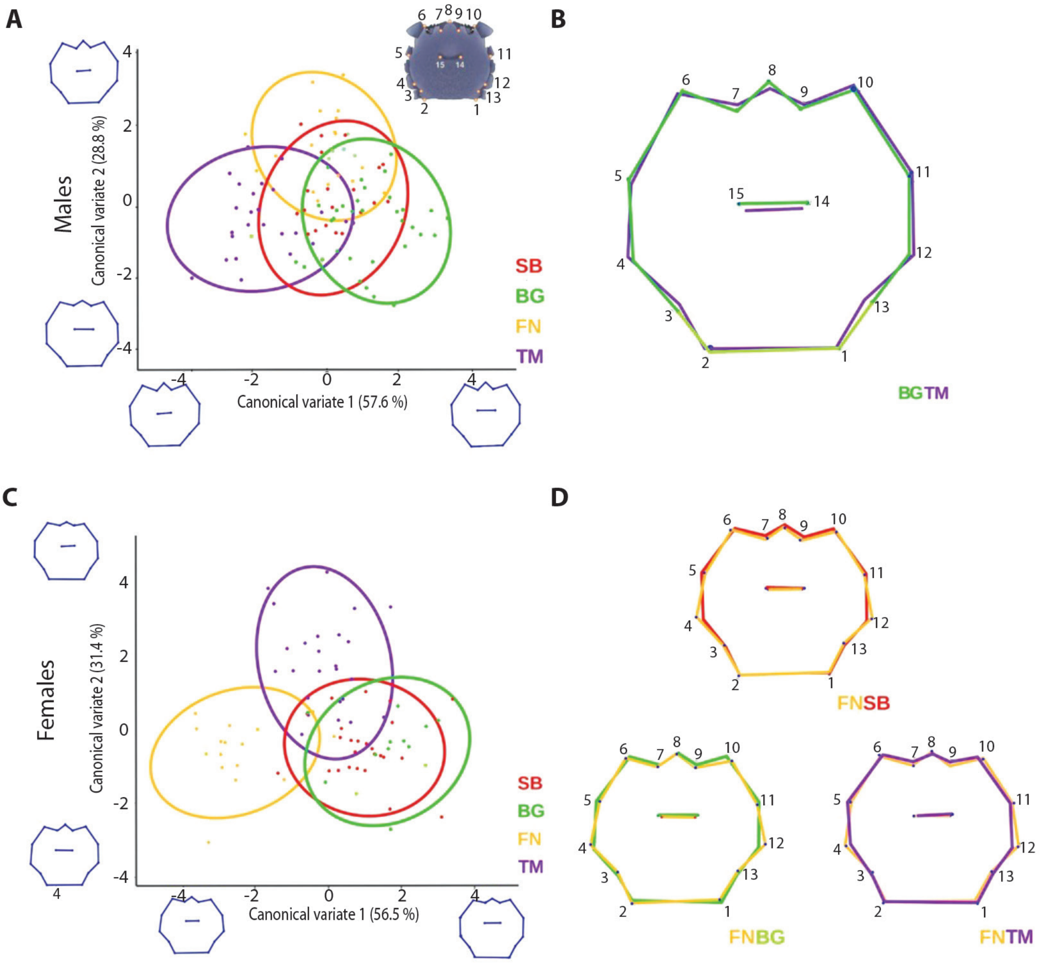

Fig. 9. Carapace morphologic variations based on canonical variable analysis (CVA). **A.-C.** Thin-plate Splines of morphological variation based on discriminant analysis (D. A). **B.-D.** Of male and female *Plagusia depressa* respectively in the areas studied. Barra Grande-BG. Suape Bay-SB. Tamandaré Beach-TM and Fernando de Noronha Archipelago-FN. 95 % confidence ellipses.

8 points), elongation of the anterior margin (1 and 9 points), and an elevation of the midpoint of the third somite (Fig. 10A, Fig. 10B).

Abdomen morphological variations in females were observed between BG and SB and, BG and TM populations ($p < 0.05$). These variables explained 87 % of the observed areas (CVA $p < 0.05$). In BG females, a narrowing of the anterior and lateral margins of the abdominal somites occurred, and a prolongation of the top of the telson (Fig. 10C, Fig. 10D). Between groups, the percentages of correct allocation were higher than 65 % in discriminant analysis (DA) ($p < 0.05$).

Right chelae shape: Right chelae shapes of male crab populations were different between all areas, according to the procrustes distance values ($p < 0.05$, Table 3). Variations in the SB population were due to a shortening of lower and upper attachment points of carpus with manus (1and 7 points) and a thickening of the convex point of the upper manus region (6 point), when compared to the other sampling

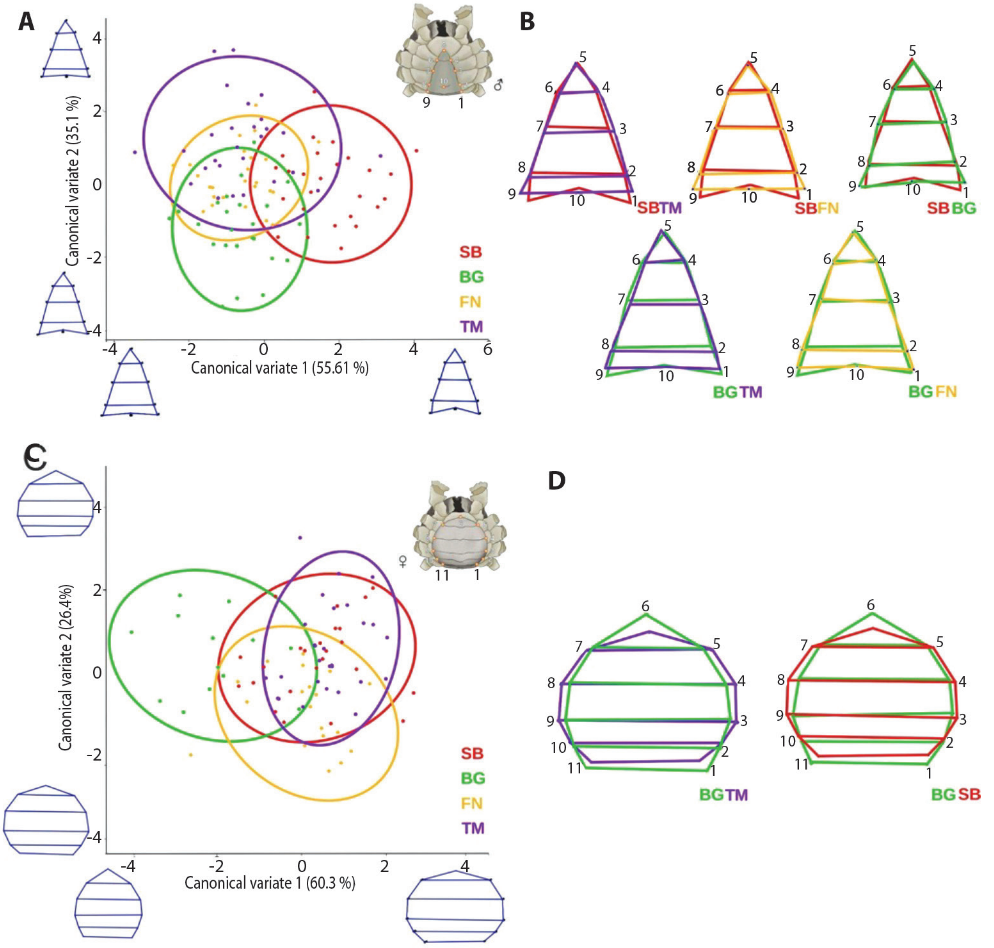

Fig. 10. Abdomen morphologic variations based on canonical variable analysis (CVA). **A.-C.** Thin-plate Splines of morphological variation based on discriminant analysis (D. A). **B.-D.** of male and female *Plagusia depressa* respectively in the areas studied. Barra Grande-BG. Suape Bay-SB. Tamandaré Beach-TM and Fernando de Noronha Archipelago-FN. 95% confidence ellipses.

areas (CVA, $p < 0.05$). BG population presented lower manus concavity (2 point) and the polex tip was more pronounced (3 point) than in the other sampling areas. Besides, the BG population presented an elongation of the lower and upper carpal attachment points with the manus (points 1and 7) (Fig. 11A, Fig. 11B).

Overall, female populations showed similar patterns to males, regarding morphological differentiation between BG and SB, and BG and FN populations ($p < 0.05$, Table 3). In this case, BG also showed an increase in the lower concavity of the manus (point 2) and the tip of the polex more pronounced (3 point) than the other study areas (Fig. 11C, Fig. 11D).

DISCUSSION

The present study provides important and new insights into the morphological variability in the reef crab *P. depressa,* a cryptic species that is not well studied. The sampling areas had different levels of protection and environmental conditions, and distinct biogeographical

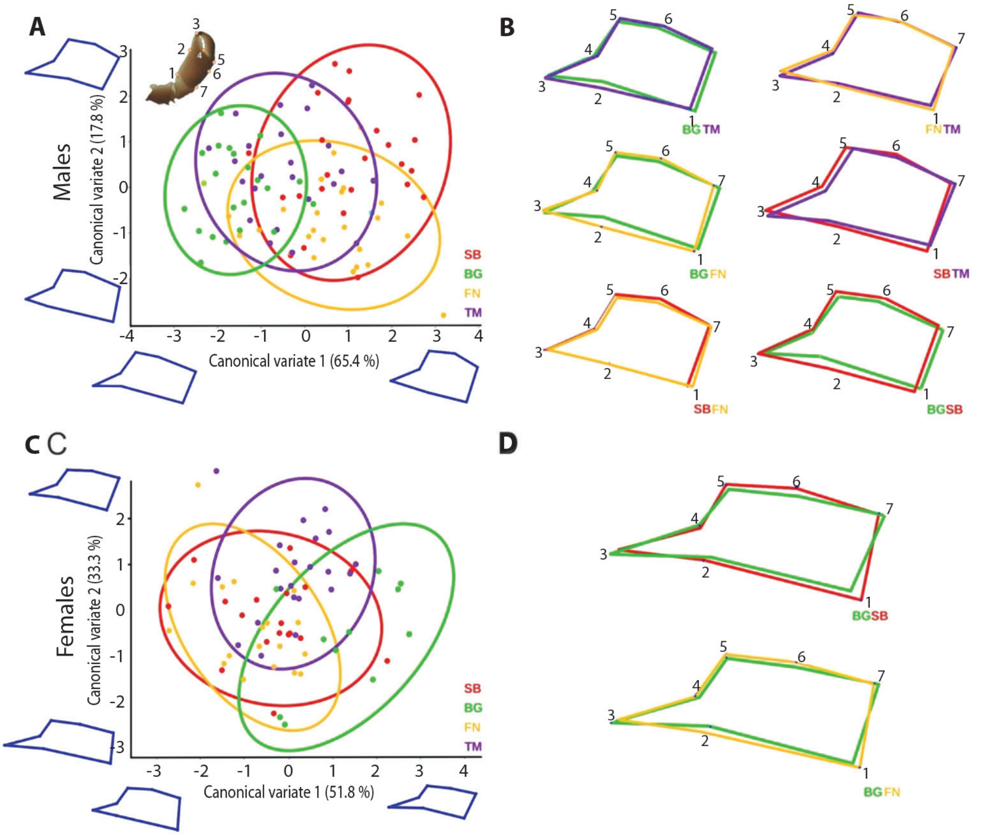

Fig. 11. Right chelae morphologic variations based on canonical variable analysis (CVA). **A.-C.** Thin-plate Splines of morphological variation based on discriminant analysis (D. A). **B.-D.** Of male and female *Plagusia depressa* respectively in the areas studied. Barra Grande-BG. Suape Bay-SB. Tamandaré Beach-TM and Fernando de Noronha Archipelago-FN. 95 % confidence ellipses.

barriers for adult and larval dispersal of this species. Overall, male crabs were morphologically different, regarding several key morphometric parameters, in the westernmost area, the Barra Grande Marine Protected Area, from all the other sampling areas. On the other hand, the carapace shape of females was different among the offshore oceanic Fernando de Noronha Marine Protect Area and the coastal areas.

Factors, processes, and biogeographic barriers affecting reef crab populations in the Barra Grande Marine Protected Area: Our results showed significant morphological differentiation patterns for male crabs in the Barra Grande Marine Protection Area (BG) for almost all the anatomical structures used in geometric morphometric analysis in relation to most of the studied areas. The most distinct morphological variations observed in crabs from BG were chelae shape, which had a more pronounced polex tip and an elongated manus in this region than in the other areas. Some studies related to brachyuran morphometry have shown that chelae are amongst the most conspicuous anatomical features of decapod crustaceans and are directly related to feeding behavior and manipulation of the food items (Marochi et al., 2017; Miyajima et al., 2012; Silva & Paula, 2008; Teschima et al., 2016). The elongated and robust chelae of males and females of *P. depressa* in BG may be associated with the aid in capturing food, the ability to reach and scrape the substrate, when it presents many irregularities, as observed for this area, since this species has preferentially herbivorous feeding habits (de Lemos et al., 2019). In addition, the BG sampling area is constituted by environments of abrasion platform types caused by the erosion of coastal cliffs that are common along this coastal area (Silva et al., 2010). Thus, BG presents protuberant areas with elevated structures, which may contribute to the need to settle and move around in the environment.

For brachyurans, several authors hypothesized that chelae size and shape are strongly influenced by sexual selection (especially in males), due to cohort behavior and disputes with other males in the population (Callander et al., 2013) as observed by Teschima et al. (2016) for *G. grapsus* populations in Brazilian oceanic islands. Another hypothesis regarding chelae shape is related to prey type, food quality and availability (Smith & Palmer, 1994). Both hypotheses may affect chelae shape in a short period, reflecting a divergent morphological intraspecific variation when compared to other anatomical structures (Grinang et al., 2019; Marochi et al., 2017), which supports our results that right chelae correspond to the highest phenotypic divergence among populations found even in geometric and linear morphometric analysis, in that it was observed through PCA that the width (RCW) and length (RCL) of the chelae influenced the separation of the study areas.

Another important point is that Barra Grande, the westernmost sampling area, is located about 550-600 km from the other areas, potentially preventing the exchange of individuals with adjacent populations since the average larval dispersal distances for marine fish and invertebrate species is about 125 km (Palumbi, 2003). The observed differences may therefore be directly due to the existence of geographic barriers. One important geographic barrier in the study area is Ponta do Calcanhar, where oceanic currents impede the dispersal of planktonic larvae from Northwest to Southeast, across this border (Thurman et al., 2013). The division of the major oceanic currents and the geomorphology at the Ponta do Calcanhar, may significantly control gene exchange between the Northern and Southern populations of individual reef crab species, as already reported for other marine invertebrate species, such as for estuarine crabs *Neohelice granulate* (Ituarte et al., 2012), fiddle crabs of genus *Uca* (Hampton et al., 2014; Rosenberg, 2001; Thurman et al., 2013) and the chaetognath *F. enflata* (Melo et al., 2020). Our study contributes to the ongoing discussion regarding the relevance of Ponta do Calcanhar as a key biogeographic barrier for planktonic dispersal in this region (Melo et al., 2020; Thurman et al., 2013). Further studies are necessary to understand if patterns of differentiation observed in our results have a genetic basis, or if they are merely phenotypic, based on real-time local forcings (i.e., if such differences are due to barriers in gene flux). Furthermore, in some cases, trophic morphology is considered to be under strong genetic control (Teschima et al., 2016; Thurman et al., 2021), while in other instances trophic variation may result from diet-induced phenotypic plasticity (Marochi et al., 2017; Smith, 2004).

Factors affecting the morphological variation of *P. depressa* in the offshore Fernando de Noronha Archipelago Marine Protected Area: Our results also indicated a pattern of variation in carapace shape and size for females in the oceanic offshore Fernando de Noronha Archipelago Marine Protected Area (FN), presenting the widest carapace and more accentuated depressions of the rostrum than in coastal populations. Many authors argued that female brachyurans having a wider carapace shape stem from a reproductive advantage, as they use this structure for energy reserves for the reproductive period and these differences may also reflect an adaptation for internal growth (e.g., gonad and muscle) (de Lira & Calado, 2013; Ferrari et al., 2011; López-Greco et al., 2004).

The morphological variation between populations may be related to phenotypic plasticity driven by environmental differences between sites (Hampton et al., 2014; Sanford & Kelly, 2011). Physical (e.g., tidal regimes and wave energy), chemical (e.g. salinity, temperature) and ecological (intra- and interspecific interactions, food availability) conditions of habitats may be responsible for morphological divergence of carapaces and phenotypic plasticity or even by epigenetic regulation (Sotka, 2012).

Crabs are ectothermic organisms that depend on environmental temperature to regulate their temperature and metabolic rates, and when they occupy semi-terrestrial habits, they suffer directly from water loss and desiccation stress (Allen et al., 2012; de Lira et al., 2015). In Fernando de Noronha, the specimens were collected on a beach in a mesolittoral zone on a rock formation that is exposed during entire low tide periods (spring and neap low tides), causing stressful conditions of desiccation to resident populations. The coastal reef areas of Tamandaré Bay, Suape Beach, and Barra Grande present considerably different habitat conditions than those reported from FN. These continental reefs are farther from the beachline, and it emerge only during low spring tides, reducing the time of exposure to high temperatures and desiccation of individuals in these areas, may explain the fact that the female carapaces do not show significant divergence between coastal areas.

Hampton et al. (2014), showed that intraspecific morphological variation found in eight species of fiddler crabs might be related to variation in humidity with water conservation in the gill chambers of female fiddler crabs *Minuca burgersi* (Holthuis, 1967). The authors infer that differences in humidity may influence gene expression and morphological variation. A similar pattern (with local pressures and factors affecting morphology) was also observed by Marochi et al. (2017), for populations of the mangrove crab *A. angustipes* (Dana, 1852) along the Brazilian coast. They based their study on differentiation in carapace and chelae morphological structures and genetic differentiation using DNA sequencing. Similarly to our study, they also found statistically significant morphological differentiation and geographic structuring between areas, despite low genetic variability and lack of phylogeographic structure. They related the observed differences to habitat selective pressure, such as differences in desiccation stress between areas. In contrast to our study, their results indicated no clear correlation of morphological (or genetic) variation with ocean currents or geographic distance. Possibly, the larval dispersal of *P. depressa* may be less effective than for *A. angustipes.* This highlights the urgent need for further studies to investigate the reproductive biology and larval dispersal patterns in these key crab species and other relevant decapods in tropical oceans, especially considering the challenges produced by climate change (Anger, 2001; Clarke et al., 2020; Rebolledo & Wehrtmann, 2016; de Santana et al., 2018).

The same pattern could also be true for *P. depressa* in the present study. Stress from desiccation due to high temperatures, together with the behavior of carapace enlargement in preparation for the reproductive period, may explain the results found in this area.

Another important point for understanding species distributions in marine environments is the exchange of individuals between populations, defined by the sum of local populations that are connected, generally by the dispersion of planktonic larvae (Marshall et al., 2010). If larval dispersal is interrupted by a geographic barrier, or if local populations respond plastically to environmental factors or are subject to different selection pressures, geographic variation may occur (Hopkins & Thurman, 2010) that can affect their survival, reproduction, and overall population health (Cadrin et al., 2014). Teschima et al. (2016), were able to observe the morphological and genetic structuring of *G. grapsus* populations among Brazilian oceanic islands through a combination of morphometric and genetic techniques. They explained this differentiation mainly by the distance between the islands and the capacity for larval dispersion through ocean currents. Fernando de Noronha archipelago is about 345 km from the coast, which makes it virtually impossible for local reef crabs to exchange with coastal populations, probably causing the morphological differences observed herein.

The results obtained in this study provided new information on several biological and ecological aspects of populations of the reef crab *P. depressa* in the WTA. Furthermore, this study brought, for the first time, information on this species in an oceanic insular environment. Intraspecific morphological structuring was identified in coastal and insular environments with different levels of anthropogenic and environmental stresses, where factors such as habitat composition and structure, and exposure time related to tidal patterns were identified as potential causes for the phenotypic plasticity of the reef crabs. Other factors such as geographic isolation, biogeographic barriers and ocean current patterns also appear to be relevant factors in the morphological differentiation between the populations studied which can directly affect demographic rates, population structure and dynamics, such as migration/recruitment patterns, and responses to environmental changes. However, studies related to genetic connectivity are still needed to better clarify if the phenotypic differences found in this study extend to issues related to gene flow within this species in the WTA. Our study and such further studies are paramount to support efforts for the conservation and management of this cryptic species and for maintaining the sustainability of marine resources in the face of changing environmental conditions and human pressures.

Ethical statement: the authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

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