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ORIGINAL PAPER

Management and conservation of the land crab *Cardisoma guanhumi* (Crustacea: Gecarcinidae) based on environmental and fishery factors: a case study in Brazil

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Abstract A mangrove ecosystem encompasses two environments, a larger flooding area with a characteristic wetland forest, and a less flooded area, more saline with little or no vegetation cover, known as hypersaline tidal flats (*apicuns*). *Cardisoma guanhumi* is a non-abundant, semi-terrestrial crab that lives mainly in *apicuns*. This environment is smaller and less impacted in comparison with mangrove forests. This study aims to investigate the spatial relation between *apicuns* and mangroves as a habitat extent of *C. guanhumi* along the Brazilian coast and its implications on fishery management and conservation status of this species in Brazil. The study was based on *apicum* and mangrove extent maps of the Brazilian coast. The maps were analyzed based on variations in latitude and environmental and socio-political aspects. Along the Brazilian coast, we found 11,721 km^2 of mangroves and 402 km^2 of *apicuns*. The habitat of *C. guanhumi* varied greatly with latitude and is interdependent of mangrove ecosystem. This latitudinal gradient and the *apicum*-mangrove relation suggest the need for different management strategies of this fishery species along the Brazilian coast. Such strategies should be used to maintain the population of *C. guanhumi* in sizes that guarantee its conservation and recovery aiming to remove this species from the category of vulnerable in the Brazilian red list of threatened species.

Keywords Apicum · Coastal ecosystem · Conservation · Small-scale fishery

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Introduction

Mangroves are a relevant coastal ecosystem. They are associated with estuarine systems and have several socio-ecological functions, including family fishery by traditional peoples (Albuquerque et al. 2014; Santos et al. 2017; Souza et al. 2018). This wetland ecosystem is influenced by the co-occurrence of sea tides and river waters and offers a unique habitat where woody angiosperm plants colonize tidal-influenced muddy sediments (Schaeffer-Novelli et al. 2016). In this environment, there are also hypersaline tidal flats (known as *apicuns* in Brazil). They are found in transition zones between rainforests and dry upland areas (Albuquerque et al. 2014). Therefore, *apicuns* are associated with less frequent tidal flooding, flat topography, high evaporation, and hypersaline soils colonized by salt-tolerant halophytes, including herbaceous shrubs and grasses (Krauss et al. 2014; Silva et al. 2020). The *apicum* is highly valuable for the mangrove ecosystem, especially for its characteristics as expansion areas of mangrove vegetation and production of nutrients for a complex and interlinked food chain (Meireles et al. 2007; Albuquerque et al. 2014).

Apicuns perform essential services to improving the life quality of traditional communities in coastal areas and the maintenance for different animal species. Despite their importance, these harsh estuarine areas have been subjected to a variety of human stresses, especially those related to aquaculture (mainly shrimp farms) and salt extraction processes (Hadlich et al. 2008; Ucha et al. 2008; Santos et al. 2014; Falcão et al. 2020). Such pressures have led to habitat loss and degradation, placing the local crab-fishery dependent population at risk, with negative effects to fishery species.

The blue land crab *Cardisoma guanhumi* Latreille, 1828 is a semi-terrestrial crab belonging to the family Gecarcinidae (Decapoda: Crustacea), distributed along the Atlantic coast from the state of Florida (United States of America) to the state of Santa Catarina, in Brazil (Ferreira et al. 2009; Gama-Maia and Torres 2016). This brachyuran species is registered from the *apicum* environment (Meireles et al. 2007; Albuquerque et al. 2014; Falcão et al. 2020) to other adjacent coastal environments (e.g., sandbanks, tropical/subtropical secondary forests and man-made vegetation, as coconut culture and others), as long as it is under the influence of estuarine processes (Costlow and Bookhout 1968; Taissoun 1974; Branco 1993; Novais et al. 2021), especially by salinity.

Along the Atlantic coast of Central and South America, *C. guanhumi* is intensively exploited in several countries, especially Puerto Rico, Bahamas, Honduras, Colombia, Venezuela, and Brazil (Carmona-Suárez 2011; Firmo et al. 2012). Unsustainable overfishing is commonly practiced (Amaral et al. 2015). In recent decades, *C. guanhumi* has experienced a sharp population decrease due to overfishing and loss or degradation of *apicum* habitats (Amaral and Jablonski 2005; Rodríguez-Fourquet and Sabat 2009; Amaral et al. 2015; Santos and Ribeiro 2019a, b). In the United States of America, the Florida Fish and Wildlife Conservation Commission considers this species biologically vulnerable (FWC 2012; Amaral et al. 2015). In Brazil, this species is categorized as Critically Endangered (CR), criteria A4bcd, according IUCN rules (see MMA 2014), due to 88% commercial production and reduction/loss of the *apicum*, considered by specialists as the more relevant environment of this species (Pinheiro et al. 2016; ICMBio 2018a, b, c). This fact reveals a need for development and implementation of effective conservation management strategies, in special those concerned to preservation of the *apicum* (Amaral et al. 2015; Pinheiro et al. 2016).

Along the Brazilian coast, *C. guanhumi* is heavily exploited and freely marketed in trade fairs, restaurants, and roadsides (Gama-Maia and Torres 2016) mainly in the northeast region of Brazil (Firmo et al. 2012; Santos et al. 2017). There, the fishery activity of this crab has a strong socio-cultural appeal, since it generates jobs and income (Barboza et al. 2008; Firmo et al. 2012; Gama-Maia and Torres 2016; Santos et al. 2017). Nevertheless, this intense exploitation is unsustainable because this species is no longer abundant and grows relatively slowly (Oliveira-Neto et al. 2014). Consequently, a relatively strong attention by the scientific community and environmental agencies has been directed towards *C. guanhumi* conservation (Gama-Maia and Torres 2016; Novais et al. 2021). The Brazilian Institute of Environment and Renewable Natural Resources (IBAMA) included *C. guanhumi* in the Brazilian list of overexploited species in 2004. In 2011, the IBAMA published the 'Proposal of a National Management Plan' for the sustainable exploitation of this species to ensure the maintenance of a standard living of local populations (Dias-Neto 2011). In 2014, *C. guanhumi* was included in the national red list of threatened species as critically endangered, according to the rules of the International Union for Conservation of Nature (MMA 2014; Pinheiro et al. 2016; ICMBio 2018a, b, c).

Brazil has one of the most extensive coastlines in the world. It extends approximately 9,000 km between latitudes 4° N and 34° S, from the north of Amapá state to the south of Rio Grande do Sul state (Klein and Short 2016). Along this extension, there are different environmental and social traits, which leads to different characteristics of exploitation and habitat sizes of *C. guanhumi*. These aspects must be considered in fishery management plans. Despite the importance of hypersaline tidal flat habitats for *C. guanhumi*, few studies have focused on these endangered habitats (Albuquerque et al. 2014; Novais et al. 2021). Therefore, studies are needed to address the ecological connection between *apicuns* and mangroves in order to assist public policies on conservation strategies, which should include the protection of the whole coastal ecosystem (Albuquerque et al. 2014; Pinheiro et al. 2016; ICMBio 2018a, b).

This study investigates the spatial relation between *apicuns* and mangroves along the Brazilian coast, considering environmental factors and fishery extraction of the land crab (*C. guanhumi*). Based on this information, the authors apply this knowledge in purpose strategies to solve the fishery management and conservation of this important fishery resource in Brazil.

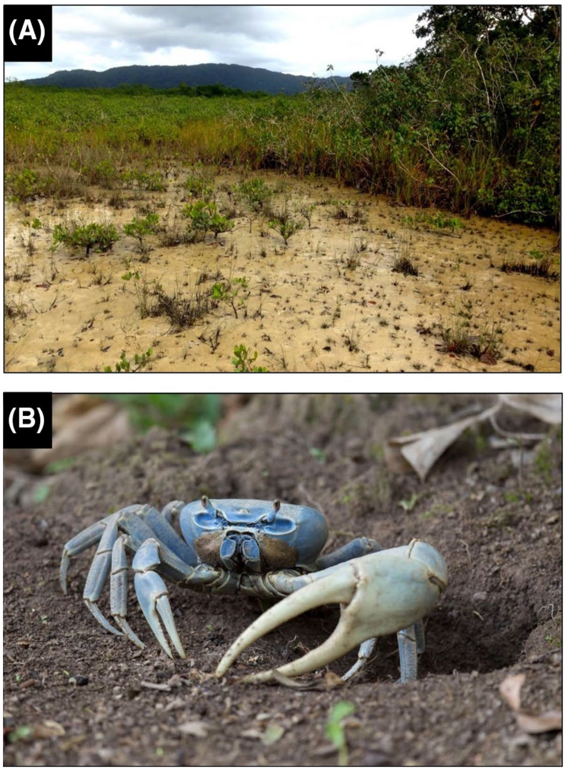

Fig. 1 Hypersaline Tidal flats (**A**) are transition coastal areas in mangroves commonly used by terrestrial gecarcinid crab *Cardisoma guanhumi* (**B**) and relevant for the conservation of this species. Photos: **A** Marcelo Pinheiro / CRUSTA – UNESP IB/CLP; and **B** Fabio Rage

Methods

Hypersaline tidal flats (Fig. 1a) are coastal transitional areas between mangroves and adjacent environments (e.g., Atlantic Forest and *restinga*, a coastal tropical and subtropical moist and broadleaf forest). The crab *Cardisoma guanhumi* (Fig. 1b) uses tidal flats as preferential habitat in estuarine areas (Albuquerque et al. 2014), due to saline dependence of their life cycle to embryonic and larval development (a pattern to species of *Cardisoma* genus — see Costlow and Bookhout 1968; Cuesta and Anger 2005). These habitats occur along almost the entire Brazilian coast, from the states of Pará to Santa Catarina, that is, a latitude ranging from 0° to 28° S (Fig. 2).

We obtained *apicum* and mangrove extent data from the research team that produced the Brazilian Mangrove Atlas (ICMBio 2018c). We analyzed data using the software GraphPad Prism®, Excel®, and Past®, considering latitudinal, environmental and related to exploitation intensity of this species, as following: (1) one-degree latitudinal gradient, from 0° to 28° S (LAT, $n = 28$); (2) Brazilian coastal states of Pará, Maranhão, Piauí, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, Bahia, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, and Santa Catarina (ST, $n = 15$); (3) coastal segments III, IV, V, VI and VII, as Schaeffer-Novelli et al. (1990, 2016) proposed (SEG, $n = 5$); (4) Brazilian geographic regions: North, Northeast, Southeast, and South (REG, $n = 4$); (5) tide amplitude (TID, $n = 3$) subdivided in macrotidal (tides > 4 m, between latitudes of 0° and 3° S), mesotidal (tides 2–4 m, between 3° S and 15° S), and microtidal (tides < 2 m, between 15° S and 34° S), according to Knoppers et al. (1999) and Magris and Barreto (2010); and (6) exploitation of *C. guanhumi* (EXP, $n = 3$), categorized as high, medium, and low exploitation, based on information on resource use

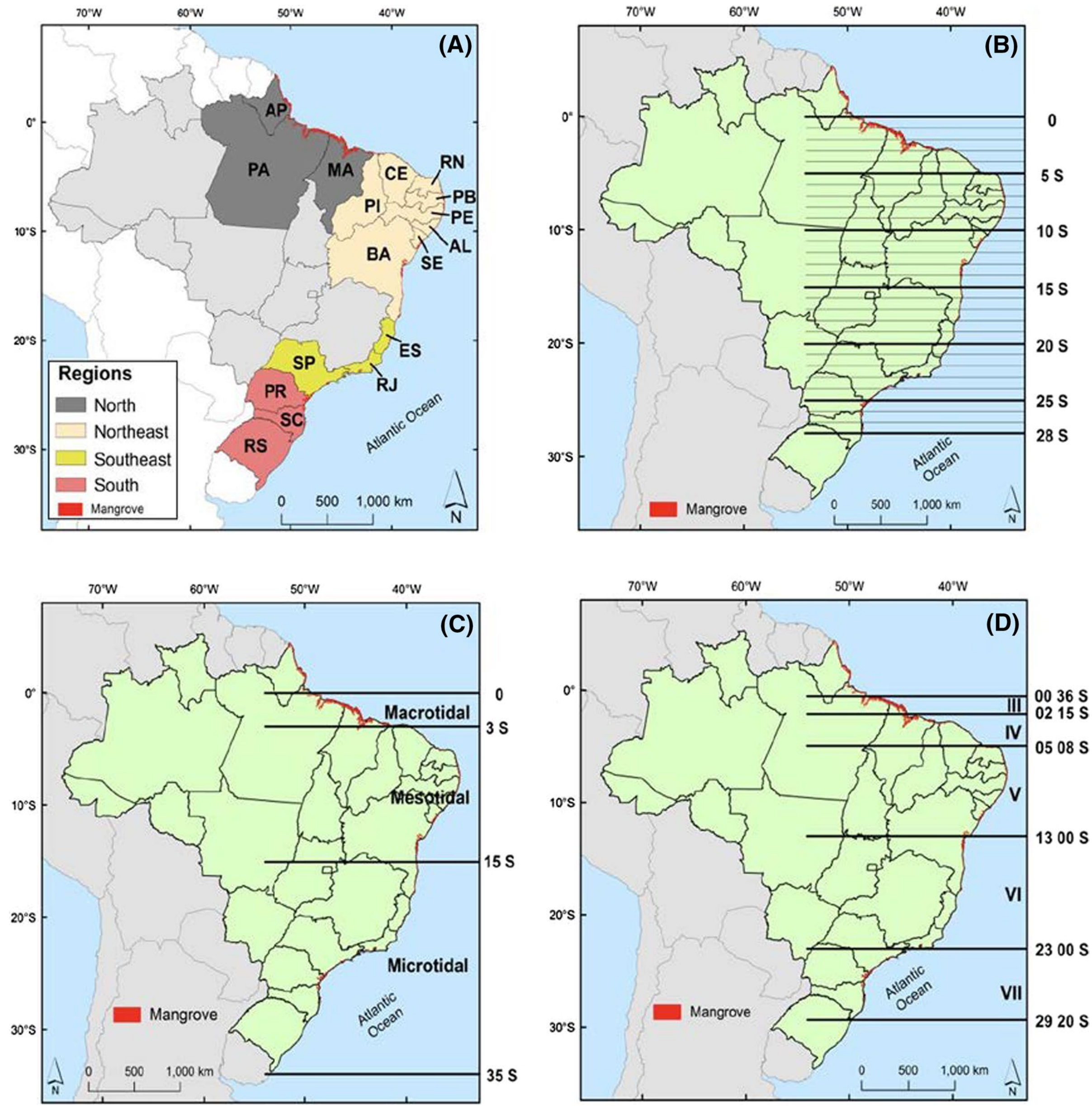

Fig. 2 Data processing and analysis based on the Brazilian regions and states (**A**), one-degree strip (**B**), tidal regimen category (**C**), and five Brazilian coastal segments proposed by Schaeffer-Novelli et al. (1990, 2016) (**D**). Where Brazilian states are represented by: *AP* Amapá, *PA* Pará, *MA* Maranhão, *PI* Piauí, *CE* Ceará, *RN* Rio Grande do Norte, *PB* Paraíba, *PE* Pernambuco, *AL* Alagoas, *SE* Sergipe, *BA* Bahia, *ES* Espírito Santo, *RJ*, Rio de Janeiro, *SP* São Paulo, *PR* Paraná, *SC* Santa Catarina, and *RS* Rio Grande do Sul

of this species suggested by Dias-Neto (2011), in a previous management proposal.

We log-transformed data on *apicum* and mangrove extents before assessing its normality and homogeneity of variances by Kolmogorov–Smirnov and Bartlett tests, respectively, in order to apply parametric tests. We performed a linear regression between *apicum* and mangrove extents along the latitudinal variation. We calculated the Pearson's correlation coefficient (r) and performed cluster analysis to investigate the relation between *apicum* and mangrove extents considering the six parameters described above (LAT, ST, SEG, REG, TID, and EXP) to identify groups of similar features.

Results

Along the Brazilian coast, we found a relatively small *apicum* extent (402 km^2) compared to mangrove extent (11,721 km^2), that is, 3.4% of the total mangrove area. We also found that *apicums* and mangroves are interconnected habitats because of a positive and high correlation between their occurrence along the Brazilian coast ($r = 0.88$; $p < 0.0001$) (Fig. 3). This relation was described by the equation $AP = 0.0365\ MA - 37.6$ ($n = 28$; $R^2 = 78.4\%$; $F = 94.61$; $p < 0.0001$), where n = number of states, AP = *apicum*, and MA = mangrove.

We found the longest areal extents of *apicums* and mangroves at low latitudes (0° to 3° S) (Fig. 4a), specifically in the states of Pará and Maranhão (Fig. 4b). Mangrove extents in these two states represent 76.5% (896,080 ha) of the total Brazilian mangrove area. These states also present the longest *apicum* extent, i.e., 76.3% (30,591 ha). Between latitudes towards the south (3º S to 28º S, covering 13 states) there was a smaller variation between mangrove extensions in relation to the greater variation of *apicum* extensions, showing a reduction of *apicum* between latitudes 3 to 23ºS, but with a later elevation of this environment between 23 to 28ºS. Therefore, Brazilian southernmost latitudes (18° S to 28° S, states of Espírito Santo, Rio de Janeiro, São Paulo, Paraná, and

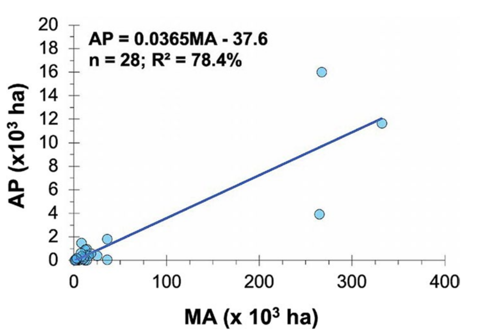

Fig. 3 Linear regression between ‘apicum’ (AP) and mangrove (MA) extents, considering data obtained along the latitudinal gradient in Brazilian coast ($n = 28$, $F = 94.61$, $p < 0.0001$)

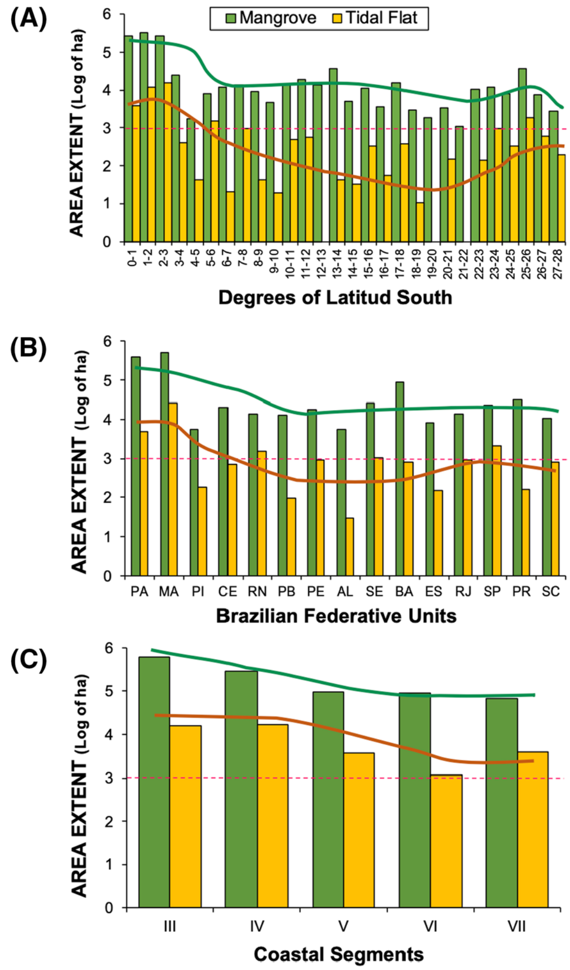

Fig. 4 Mangrove and hypersaline tidal flat extent along the Brazilian coast, considering different environments and sociopolitical factors: **A** latitudinal gradient; **B** federative units (states); and **C** coastal segments. Where: dashed red line, mean value in each condition; curved green line (mangrove extent) and brown line (hypersaline tidal flat extent), based on the moving average of the data for each case

Santa Catarina) also have small extents of *apicums* (10.5%; 4,206 ha) and mangroves (7.3%; 85,639 ha). As a general pattern, the longest *apicum* and mangrove extents occur in the northern part of Brazil, reducing in mid-latitudes and increasing a little in the southernmost latitudes. *Apicum* extents are more pronounced in the coastal segments III and IV (0º a 5º S), with a decrease and similarity between the segments V to VII (latitudes from 5° to 28° S), especially in segment VI where their more reduced extent was registered (Fig. 4c). This reduced *apicum* extent was

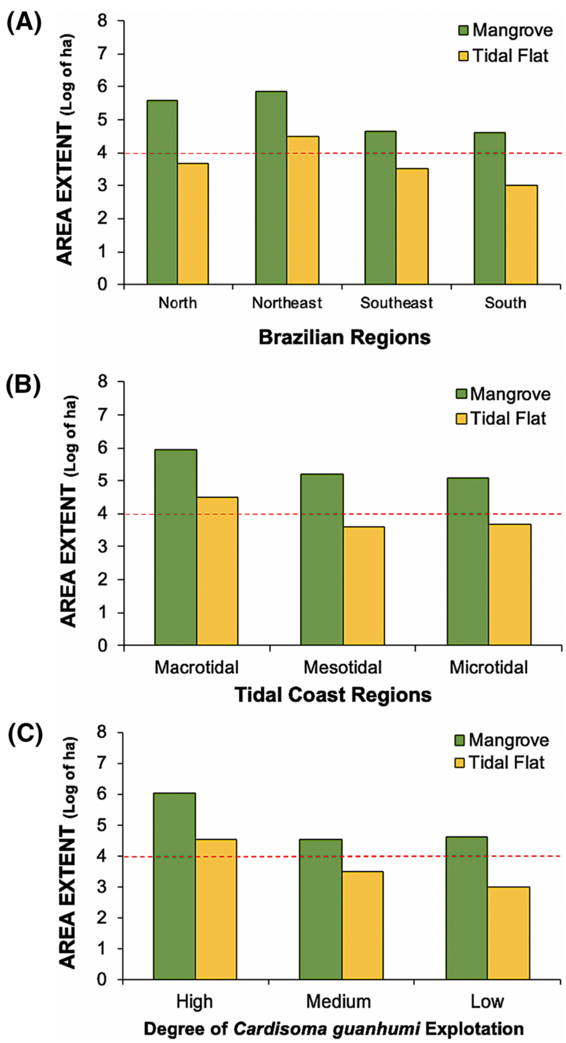

Fig. 5 Mangrove and hypersaline tidal flat extent along the Brazilian coast, considering different environmental and socio-political factors: **A** federative Brazilian regions; **B** tidal amplitude coast; and **C** degree of exploitation of *C. guanhumi*. Where: dashed red line, mean value in each condition

mainly confirmed in many areas between the cities of Salvador (Bahia state: 12º S) and Rio de Janeiro (Rio de Janeiro state: 22º S).

In the Northern and Northeastern regions (Fig. 5a), corresponding to macrotidal and mesotidal coasts (Fig. 5b), we found the longest *apicum* and mangrove extents. In contrast, in the Southeastern and Southern regions, the extent of both habitats decreases associated with the microtidal coast. Despite this pattern, similar as that of the previous analysis, there is a greater variability when extents are analyzed considering latitudinal gradient and division of states.

We observed a distinct pattern for the exploitation degree of *C. guanhumi* (Fig. 5c). We found the longest habitat extent where there is no exploitation. The absence of *C. guanhumi* exploitation is probably due to its low abundance in states located in the north (Pará, Maranhão and Piauí), which, in turn, concentrate the longest areas of *apicuns* and mangroves.

The most statistically significant correlation was between latitudinal gradient and *apicum* ($r = -0.45$; $p = 0.017$) and mangrove extents ($r = -0.54$; $p = 0.003$) (Table 1). Only mangrove extent presented negative correlation with states and coastal segments. Longer extents of mangrove and *apicuns* were at lower latitudes, increasing towards the northern part of Brazil, comprising ten states (from Pará to Bahia). It mainly corresponds to the coastal segments III to V (North and Northeast regions, where we find macrotidal and mesotidal amplitudes). On the other hand, we found a shortening of mangroves and *apicuns* extents towards the southern part of Brazil mainly in three states: São Paulo, Paraná, and Santa Catarina, which corresponds to the South and Southeast regions of Brazil and to the coastal segments VI and VII (microtidal amplitude). In Rio Grande do Sul, the southernmost state of Brazil, salt marshes replace mangroves.

Table 1 Parametric correlation coefficient of Pearson (r) calculated to investigate the relationship between mangrove and tidal flat extent and each one of the environmental and socio-political factors analyzed (*$p < 0.05$)

Factor	n	Mangrove (M)		Tidal flat (AP)	
		r	P-value	r	p-value
Latitudinal gradient (LAT)	28	– 0.54	0.003*	– 0.45	0.017*
Federative units (ST)	15	– 0.55	0.033*	– 0.43	0.112
Coastal segments (SEG)	5	– 0.89	0.045*	– 0.84	0.075
Brazilian regions (REG)	4	– 0.70	0.303	– 0.36	0.638
Coastal tide amplitude (TID)	3	0.89	0.298	0.85	0.351
Exploitation of *C. guanhumi* (EXP)	3	0.86	0.336	0.89	0.299

Weighted tidal flat extent (TFE) can be a good index to study the habitat availability for *C. guanhumi* in each Brazilian state. It supports decision-makers on planning fishery management (Table 2) and ensures easier strategies to be implemented at a state level. It is important to highlight that the areas with the best habitat condition for *C. guanhumi* are the same where there are a high weighted tidal flat and mangrove extents (TFE and MAE, respectively), considering their interconnectivity. Open fishery areas (OFA) were confirmed with a TFE ≥ 15,000, indicating the best habitat availability for *C. guanhumi* and corresponding to distinct fishery potentials (MFP: medium fishery potential when 15,000 < TFE < 18,000; and HFP: high fishery potential when TFE ≥ 18,000). On the other hand, in cases of TFE ≤ 9,000.

There are poorer habitat conditions. We found the lowest TFE values in five Brazilian states (Espírito Santo, Rio de Janeiro, São Paulo, Paraná, and Santa Catarina) (Fig. 6). In such cases, the density and size of *C. guanhumi* populations tend to decrease, revealing a management directed to conservation instead of exploitation.

We performed a cluster analysis of Brazilian states (Fig. 7) based on the relation among the six parameters evaluated for *Cardisoma guanhumi* (single linkage by Bray–Curtis similarity index, with a

Table 2 Data established to each parameter studied (*UF* federative unit, *SEG* coastal segment, *REG* Brazilian region, *TID* tidal coast, *EXP* exploitation degree), based on tidal flat and mangrove areas, and the combined analysis (average) to obtain each index (*MAE* mangrove extent, *TFE* tidal flat extent)

Areas	Federative unit	Parameters					Index
		UF	SEG	REG	TID	EXP	
Mangroves (MAE)	PA	3.91	5.97	3.91	8.65	10.94	6.67
	MA	5.05	5.97	6.96	8.65	10.94	7.51
	PI	0.06	2.94	6.96	8.65	10.94	5.91
	CE	0.20	2.94	6.96	1.63	10.94	4.53
	RN	0.14	0.95	6.96	1.63	10.94	4.12
	PB	0.13	0.95	6.96	1.63	10.94	4.12
	PE	0.17	0.95	6.96	1.63	10.94	4.13
	AL	0.06	0.95	6.96	1.63	10.94	4.11
	SE	0.27	0.95	6.96	1.63	10.94	4.15
	BA	0.90	0.93	6.96	1.63	10.94	4.27
	ES	0.08	0.91	0.44	1.17	10.94	2.71
	RJ	0.14	0.91	0.44	1.17	0.36	0.6
	SP	0.22	0.66	0.44	1.17	0.36	0.57
	PR	0.31	0.66	0.42	1.17	0.42	0.59
	SC	0.10	0.66	0.42	1.17	0.42	0.55
Tidal flats (TFE)	PA	0.05	0.16	0.05	0.32	0.36	0.19
	MA	0.26	0.16	0.31	0.32	0.36	0.28
	PI	0.00	0.16	0.31	0.32	0.36	0.23
	CE	0.01	0.16	0.31	0.04	0.36	0.18
	RN	0.02	0.04	0.31	0.04	0.36	0.15
	PB	0.00	0.04	0.31	0.04	0.36	0.15
	PE	0.01	0.04	0.31	0.04	0.36	0.15
	AL	0.00	0.04	0.31	0.04	0.36	0.15
	SE	0.01	0.04	0.31	0.04	0.36	0.15
	BA	0.01	0.02	0.31	0.04	0.36	0.15
	ES	0.00	0.01	0.03	0.05	0.36	0.09
	RJ	0.01	0.01	0.03	0.05	0.03	0.03
	SP	0.02	0.04	0.03	0.05	0.03	0.03
	PR	0.00	0.04	0.03	0.05	0.01	0.03
	SC	0.01	0.04	0.03	0.05	0.01	0.03

All values are expressed in hectares × 10^5

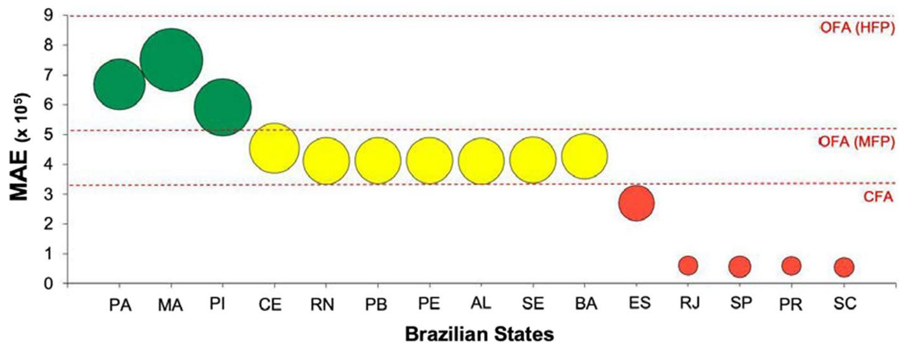

Fig. 6 Tidal Flat Extent (TFE weighted index × 10^5, as diameter) in function of the Mangrove Area Extent (MAE weighted index × 10^5, y-axis) along the Brazilian Federative Units, considering three groups of management proposed to *Cardisoma guanhumi*: open fishery areas (OFA), considering the fishery potential (high, HFP; and medium, MFP); and closed fishery areas (CFA)

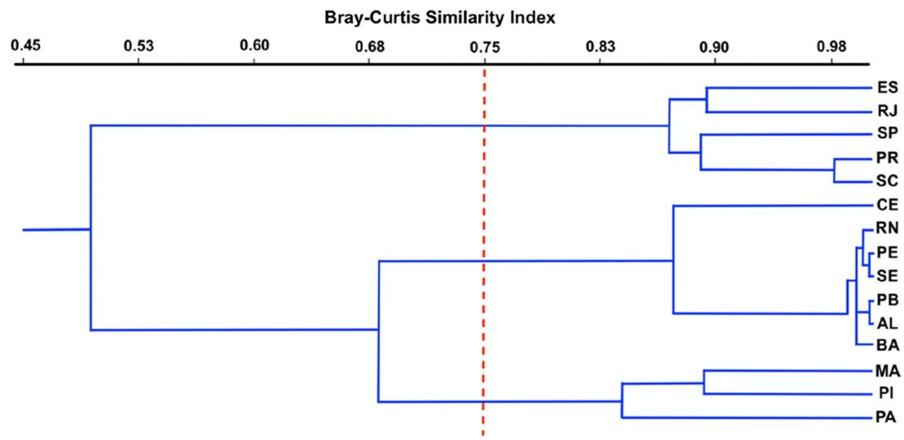

Fig. 7 Cluster analysis of the Brazilian Federative States based on relationship involving hypersaline tidal flat extent by federative units, coastal segments, Brazilian region, tidal coats and exploitation degree of *Cardisoma guanhumi* (single linkage by Bray–Curtis similarity index, with a cophenetic correlation coefficient = 0.92)

cophenetic correlation coefficient of 0.92). Considering a threshold of 0.75, we obtained three groups of Brazilian states. This confirms the same categories as Fig. 6 and Table 3 show: Group 1 (three states: Pará, Maranhão, and Piauí), Group 2 (seven states: Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, and Bahia), and Group 3 (five states: Espírito Santo, Rio de Janeiro, São Paulo, Paraná, and Santa Catarina).

Discussion

Mangroves develop better where the suitable topography is subjected to large tidal ranges and large inputs of river discharge, rainfalls, nutrients, and sediments, which are mostly found at low latitudes (Schaeffer-Novelli et al. 1990). For *apicuns*, low tidal flooding, associated with an evaporative environment, water deficit, and input of sandy sediments, seems to be the primary controlling factors for the formation of such hypersaline coastal wetlands (Albuquerque et al. 2014). In Brazil the low extent of *apicuns* is explained by restricted abiotic conditions (e.g., temperature, rainfalls, tidal amplitude, geomorphology, among others), which are required for their formation. Besides of these factors, the presence of human activities can also affect their environmental loss and degradation. Therefore, when studying the fauna associated with these habitats, it is fundamental to consider the latitude gradient along with other environmental factors. This is because the habitat extent for the fauna can greatly change along with latitude in the Brazilian coast, impacting species abundance and

Table 3 Summary of habitat assessment along the Brazilian coast (TFE, tidal flat extent weighted; and MAE, mangrove area extent weighted), proportion MAE/TFE and its implication to fishery and conservation of the land crab *Cardisoma guanhumi*

Federative unit	TFE	MAE	Management recommendation
PA	0.19	6.67	OFA (HFP)
MA	0.28	7.51	
PI	0.23	5.91	
CE	0.18	4.53	OFA (MFP)
RN	0.15	4.12	
PB	0.15	4.12	
PE	0.15	4.13	
AL	0.15	4.11	
SE	0.15	4.15	
BA	0.15	4.27	
ES	0.09	2.71	CFA
RJ	0.03	0.60	
SP	0.03	0.57	
PR	0.03	0.59	
SC	0.03	0.55	

OFA open fishery areas, *CFA* closed fishery areas, *HFP* high fishery potential, *MFP* medium fishery potential)

All values are expressed in hectares × 10^5

density. This fact is important for the management of fishery species because a variety of commercially important species colonizes these habitats, especially *C. guanhumi*, which is exclusively found in *apicuns*.

Brazil has a relatively small extent of hypersaline *apicuns*, despite presenting the second largest mangrove area in the world (Spalding et al. 2010). In general, the shorter *apicum* extent explains the lower density of *C. guanhumi*. However, Carqueija (2008, *apud* Dias Neto 2011) recorded 1.95 crab m^{-2} in the Northeast region, i.e., nine times higher than that Oliveira-Neto et al. (2014) found in the South (0.22 crab m^{-2}). This needs to be considered in the management of this species (Table 3).

Therefore, this study shows the existence of a statistical relation of dependence between *apicum* and mangrove. This relation was only qualitatively described in previous studies (Bigarella 1947, 2001; Schaeffer-Novelli 2002; Ucha et al. 2008; Hadlich et al. 2010; Albuquerque et al. 2014). According to these authors, the existence of mangroves is a primary condition for the formation of hypersaline *apicuns*, which is in turn related to the deposition of fine sands on the mangrove's root structures during spring tides (Bigarella 1947; 2001; Cintrón et al. 1978; Schaeffer-Novelli 2002). This consistent sediment input raises the topographic level in relation to the mangrove, preventing the entrance of tide waters and accumulating salt (Vieillefon 1969; Pellegrini 2000 *apud* Albuquerque et al. 2014).

On the other hand, Ucha et al. (2004) and Ackermann et al. (2006) considered the input of sediments from higher adjacent areas (coastal tablelands) as the major factor for the formation of *apicuns*. In fact, Meireles et al. (2007) found that, in several estuaries of the Northeast of Brazil, the sand input takes place through wind flows, when dunes migrate toward mangrove estuarine channels, producing sandbars responsible for the formation of *apicuns*. We believe that both flows of sediment, i.e., tides or adjacent elevated areas, are important for the formation of *apicuns*. In any case, they only occur with the presence of mangroves, as we have found along the entire Brazilian coast.

C. guanhumi lives mainly in *apicuns*, instead of in mangroves. However, as *apicuns* are interrelated with mangroves, mangroves are indispensable for crab survival. In accordance with our findings, Govender and Thomlinson (2010) found that *C. guanhumi* galleries occur within a 300-m buffer zone from mangrove forests in estuarine areas where strict environmental requirements are met. Moreover, the geographic distribution of *C. guanhumi* also follows the geographic distribution of mangroves in the American continent (Botelho et al. 2001; Dias-Neto 2011). The interconnection between these ecosystems highlights the importance of assessing both habitats when addressing management and conservation of *C. guanhumi*.

In Pará, *C. guanhumi* is associated with a low population density. Its presence in Maranhão and Piauí, in turn, still needs confirmation (Lima et al. 2009). According to these authors, there are no records of this species being sold in open markets along the northern coast of Brazil. We believe this is due to the decrease in salinity promoted by the Amazonas River, which limits the development of larval stages of *C. guanhumi*. Studies that corroborate this fact have also shown that plumes from the Amazonas River reduce the water salinity (< 5) and the maximum turbidity zone near the coast (Fontes et al. 2008, 2011).

The comparison of areas with exploitation activity shows a clear tendency of high exploitation in large areas with *apicuns* and mangroves. This can be attributed to the higher abundance of habitat available for this species, as well as to stricter environmental factors necessary to maintain fishery potential. Corroborating our results, a previous study (Dias-Neto 2011) has pointed out that the abundance of *C. guanhumi* is not expressive in the South region of Brazil, while the fishery potential in the North and Northeast regions is high.

In the Brazilian coast, the best habitat extents for *C. guanhumi* were found in the states of Pará and Maranhão. These places recorded the highest TFE and MAE (Fig. 6; Table 2). This is probably the reason that this part of the coast supports the highest densities of *C. guanhumi* in Brazil (see Dias-Neto 2011), as well as a high degree of exploitation. The long extent of these habitats in this area can be explained by environmental and anthropogenic factors, such as high tide, high temperature, and high solar radiation, large estuaries and deltas, great volumes of rainfalls, and low human impact on these ecosystems. These factors promote a favorable condition for the development of mangrove ecosystems, which, in turn, can promote the formation of *apicum* habitats by the action of sedimentation (Albuquerque et al. 2014). In general, the largest mangrove covers are found in areas with high levels of rainfalls, macrotidal regimes (Schaeffer-Novelli et al. 1990), and presence of river deltas, where the water flows directly into the ocean and creates new portions of land through active processes of sediment deposition (Spalding et al. 2010). Additionally, the states of Pará, Maranhão, and Piauí comprise the world's largest contiguous mangrove systems (Spalding et al. 2010; Nascimento et al. 2013). These three states presented a TFE $\geq$ 18,000, i.e., favorable for *C. guanhumi* fishery activity.

Similar findings were also found for seven states (Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, and Bahia), however with intermediate TFE values (15,000 < TFE < 18,000) compared to those of Pará and Maranhão states (Fig. 6; Table 3). Therefore, these eight Brazilian states present few habitats for *C. guanhumi*. This indicates that this species has enough habitats, which leads to more frequent fishery activities despite favorable environmental conditions for the development of *apicuns*, such as high temperature and the dry season (Albuquerque et al. 2014), and dunes (Meireles et al. 2007). In some Brazilian regions such as the Northeast, human pressure and degradation are important issues because they promote decreases in *apicum* extents due to the construction of reservoirs for aquaculture, which causes loss of habitats in seven states (Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, and Bahia) where this activity is highly intensive (Meireles et al. 2007).

In the Brazilian Northeast, 23% of mangroves are in environmentally protected areas (Magris and Barreto 2010), which contributes to the loss of both habitats in this coastal region. For *apicuns*, before the new Brazilian Forest Code (Federal Law no. 12.651 of May 25, 2012) (Brasil 2012), the scenario was worse because of an ambiguous interpretation of legislation that considered *apicuns* as not belonging to mangrove areas, leading to a strong degradation of *apicuns* (Schaeffer-Novelli 2002; Albuquerque et al. 2014). Although the new Forest Code included *apicuns* as ecologically sustainable use areas, it has also allowed an occupation rate of 10–35% by shrimp farms and salt extraction enterprises, respectively (Albuquerque et al. 2014). Past losses of these habitats certainly greatly affected the population of *C. guanhumi*.

Decreases in populations of *C. guanhumi* and of other crustaceans in mangrove areas have been previously reported (Alves and Nishida 2003; Costa-Neto 2007; Souto 2007; Firmo et al. 2012; Pinheiro et al. 2016; Santos et al. 2017). Such decreases have been attributed to habitat losses (Firmo et al. 2012) due to conversion of *apicuns* into other anthropic activity areas, as previously mentioned (Schmidt et al. 2013). Globally, the loss and fragmentation of habitats are pointed out as the main cause of biodiversity loss, which was expected here considering the small extent of *apicuns* submitted to these anthropic impacts. In the case of *C. guanhumi*, changes can promote decreases in abundance, density, and population structure, affecting its conservation status and the fishery activity. This can explain the high decrease in the production of *C. guanhumi* in some Brazilian states, such as Sergipe, the only state with official fishery statistics for this species. Official statistics recorded an 88% decrease in its production in between 1994 and 2007 (Dias-Neto 2011).

Although the fishery activity of *C. guanhumi* could be allowed in Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, and Bahia due to intermediate TFE values (see Table 3), other rules supporting sustainable fishery of this resource should be implemented, for example a law on fishing closure periods (Dias-Neto 2011) and intensified supervision and proper management of its natural population aiming to provide an efficient sustainable use of this species and ensuring the continuity of exploitation (Pinheiro and Fiscarelli 2001; Santos et al. 2016). Other management strategies, such as a fixed exploitation rate (capturing the same percentage of stocks, but allowing a reproductive and spawning quota) and a fixed escapement rule (a same number of crabs spawning each year to establish a stock after harvest), should be also considered. Such strategies can assure future generations of this land crab. In fact, it is the same procedure as indicated for the management of the crab *Ucides cordatus* (Santos et al. 2016) in mangrove areas.

Although our study showed that the latitudinal gradient is the major factor correlating *apicum* variability to mangrove extents along the Brazilian coast, we also highlight a similar pattern of variation in relation to other factors, underlining the importance of considering them in the management of the crab fishery species found in these habitats. In Brazil, the federal, state, and municipality-based governmental agencies carry out fishery management. In relation to *C. guanhumi*, many management rules, such as fishery closure policy, for example the IBAMA Ordinance no. 034/2003-N, IBAMA Ordinance no. 53/2003, are implemented at regional and state levels (Dias-Neto 2011). Therefore, the weighted analysis of these habitat extents considering the state level (Table 2; Fig. 6) is more appropriated to delineate management strategies than analyses considering other factors such as latitude, region, or exploitation level.

This is related to the small extent of *apicuns* and specific environmental conditions, and particularly the low temperatures in these states, which are unfavorable for this land crab species and the formation of its habitat. *C. guanhumi* has a limited distribution because of restrictions in terms of groundwater and soil temperatures (required temperature range: 20–30°C) (Silas and Sankarankutty 1960; Herreid and Gifford 1963; Wolcott 1988; Govender et al. 2008; Govender and Thomlinson 2010).

Although adults are capable of supporting extreme conditions of acidity, oxygenation, and salinity (Pinder and Smits 1993), typical of *apicuns*, experiments in laboratory have shown that larvae mortality occurs from 20°C, increasing the number of survivors only after 25°C (Costlow Jr. and Bookhout 1968). Oliveira-Neto et al. (2014) argued that the mortality of larvae due to low temperatures could be the main factor limiting the occurrence of *C. guanhumi* in southern Brazil. This means that the lower temperatures found in the South and Southeast regions of Brazil during the winter season (states of Rio de Janeiro, São Paulo, Paraná, and Santa Catarina) can limit the development of large populations of *C. guanhumi*. In this scenario, considering the findings of the present study (TFE ≤ 9,000 in the South/Southeast of Brazil), as well as the biological limitations of this species, such as slow growth, high number of molts to achieve the maximum size (approximately 60), high longevity (11–13 years), larval mortality (< 20ºC), late sexual maturity (1.5–4 years) (Costlow and Bookhout 1968; Henning 1975; Botelho et al. 2001; Wedes 2004), the fishery exploitation of *C. guanhumi* in the South/Southeast regions of Brazil cannot be recommended, and these areas could be preserved to assure the conservation bank of this species (Table 3). In the states of Paraná and Santa Catarina, *C. guanhumi* occurs at low densities and does not represent a significant fishery stock (Dias-Neto 2011). However, in the Southeast region of Brazil, some areas in Rio de Janeiro and São Paulo have an expressive fishery activity of *C. guanhumi*, mainly in the Restinga da Marambaia (Rio de Janeiro state) and Ilha Comprida (São Paulo state).

The well-known fishery pressure of land crabs and the ongoing degradation and reduction of its habitat highlight the need to develop and implement sustainable management and protection strategies (Firmo et al. 2012). Considering the habitat assessment carried out in our study and the current conservation status of *C. guanhumi* in the Brazilian coast, we suggest a regional management based on cluster analysis using data obtained at a state level (Fig. 7) and the definition of sustainable fishery and conservation areas (Table 3). In summary, fishery can be allowed in Pará, Maranhão, and Piauí states (latitudes varying from 0° N to 3° S) due to both large extensions of mangrove and *apicum* areas (TFE ≥ 15,000) together with favorable environmental conditions of temperature for this species and its habitat, which enables the colonization of large populations of *C. guanhumi*. Fishery of this land crab can be also allowed in the states from Ceará to Bahia (latitude variation of 3º S to 18º S), but with additional management strategies for sustainable use due to intermediate *apicum* and mangrove extensions (15,000 < TFE < 18,000). On the other hand, in the states between Espírito Santo and Santa Catarina (18º S to 28º S), the *apicum* and mangrove extent ratio is low (TFE ≤ 9,000), with multiple conservation units. There, conservation should be prioritized against fishery, especially because this region combines two features that are inappropriate to this species (small habitat extent of apicuns and mangroves and low temperatures), which can explain the low levels of abundance and density of this species in these states.

Santos and Ribeiro (2019a, b) also suggested implementing a regional management plan establishing rules for a sustainable use of *C. guanhumi*, some of them proposed by Govender and Thomlinson (2014) to establish no-take zones for *C. guanhumi* in Puerto Rico estuaries due to a high urban pressure on the small-extent remaining habitats of this species, which meets the strict environmental requirements of this species.

According to Albuquerque et al. (2014) is essential a better explanation about the ecological relationship between hypersaline tidal flats (HTFs) and other wetlands to improve public policies and conservation laws on the protection of all coastal ecosystems. Considering more regional and local scales, the preservation of native forests and restinga shrubs that border rivers and water bodies also appear to be fundamental for the conservation of *C. guanhumi* (Novais et al. 2021). According this authors, other environmental estuarine areas changed to other human uses (e.g., pastures, the successional stage grassland scrub and coconut-tree plantations), present less favorable conditions to establishment of this species.

Conclusions

Our study is the first to record the quantitative dependence between *apicum* and mangrove extents. It highlights that it is not only important to consider assessments of the specific habitat of an animal species, but also of neighboring ecosystems, when addressing animal conservation and management in dynamic and interdependent coastal landscapes. This has a major application to fishery species found in coastal and estuarine habitats, such as endangered species listed in the Brazilian red list of threatened species developed between 2010 and 2014.

In the Brazilian coastal landscape, the habitat of *C. guanhumi* greatly varies with latitude and is interdependent on mangrove ecosystems. We conclude that this relation and the latitudinal gradient must be considered in creating different management strategies of this fishery species along the Brazilian coast, and that management at a state level should be considered. In this view, we recommend the continuity of fishery of *C. guanhumi*, complying with the Brazilian legislation, from the states of Pará (1º N latitude) to Bahia (18° S latitude), but considering additional strategies for sustainable use in the states of Pará, Maranhão, and Piauí, where the habitat extent is smaller. By contrast, conservation should be prioritized in face of exploitation in the states from Espírito Santo (18° S latitude) to Santa Catarina (28° S latitude), which coincides with smaller habitat extents, which do not support a large abundance of *C. guanhumi* for commercial exploitation. These recommendations should also be accompanied by policies, laws, and efforts to conserve and recover the degraded habitats of *C. guanhumi*. Social and environmental programs with the local inhabitants that capture this species should also be implemented. These strategies should be applied to maintain the population of *C. guanhumi* at sizes that guarantee its conservation and recovery, focusing on the future removal of this species from the category of vulnerable in the Brazilian red list of threatened species.

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Declarations

Conflict of interest The authors have not disclosed any competing interests.

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