Journal of Experimental Marine Biology and Ecology 508 (2018) 1–12

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Reassessment of the franciscana *Pontoporia blainvillei* (Gervais & d'Orbigny, 1844) distribution and niche characteristics in Brazil

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ARTICLE INFO

Key-words:
Cetaceans
Distributional gaps
Environmental suitability
Geographic range
Western South Atlantic Ocean

ABSTRACT

The franciscana (*Pontoporia blainvillei*) is the most threatened small cetacean of South America. The species is endemic to coastal waters of the western South Atlantic Ocean, where it is distributed from Itaúnas (Brazil) to Golfo San Matias (Argentina). Its range was divided in four Franciscana Management Areas (FMAs) for conservation purposes. However, the distribution of the franciscana is not continuous along its range, with two hiatuses proposed in southeastern Brazilian coast. The absence of franciscana records in these regions has been confirmed by multiple years of research, however the reasons for this discontinuous distribution is not well understood. In this study, information on the distribution of the franciscana in south and southeastern Brazil is updated and new limits for FMAs are proposed. NicheA 3.0 software was used to investigate the environmental suitability of distributional gaps in relation to four weakly correlated, allegedly relevant descriptors of franciscana's distribution. In total, 788 records from dedicated aerial and boat surveys and bycatch were used to verify and to confirm the new FMAs limits proposed by franciscana's experts previously. The distributional gaps were reshaped and defined as following: Gap I from Piraquê-Açu River Mouth, Santa Cruz (19°57′S) in the state of Espírito Santo to Barra de Itabapoana (21°18′S) in the state of Rio de Janeiro; and Gap II from Armação dos

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https://doi.org/10.1016/j.jembe.2018.07.010
Received 19 June 2017; Received in revised form 17 July 2018; Accepted 28 July 2018

Búzios (22°44′S) to Piraquara de Dentro (22°59′S) in Rio de Janeiro. The ecological niche model indicated that distributional gaps are inside franciscana's fundamental niche, and are relatively suitable in terms of salinity, temperature, diffuse attenuation and bathymetry. However, the narrow of continental shelf seems to be the main factor explaining the absence of franciscanas in the distributional gaps as well as for the differentiation of some of the FMAs proposed. Narrowness of continental shelf seems to be intensifying the dynamics of biotic interactions promoting food competition for example, and/or causing geographic limitation to maintain minimal viable population size in present or past times periods.

1. Introduction

The franciscana *Pontoporia blainvillei* (Gervais & d'Orbigny, 1844) is the most threatened small cetacean of South America (Secchi et al., 2003a). Mortality in gillnets have been impacting franciscana dolphins throughout their range for at least 50 years (e.g. Ott et al., 2002; Prado et al., 2013, 2016; Secchi et al., 2003a, 2003b), compromising the viability of its populations (Kinas, 2002; Secchi, 2006). The franciscana faces a high risk of extinction and is listed as "Vulnerable" on a global scale by IUCN (Zerbini et al., 2017), while regionally in Brazil it is officially listed as "Critically Endangered" (MMA, 2014).

The franciscana is endemic to coastal waters of Brazil, Uruguay, and Argentina. Currently, the species occurs from Itaúnas (18°25′S), in the state of Espírito Santo, southeastern Brazil (Siciliano et al., 2002) to Golfo San Matias (41°10′S), Rio Negro, Argentina (Crespo et al., 1998). Early studies showed evidence that franciscana is not continuously distributed along its range in Brazil (Siciliano et al., 2002). Many years of bycatch monitoring, beach surveys for stranded animals and aerial surveys confirms the existence of two distributional gaps: (1) from Regência (19°40′S), in Espírito Santo, to Barra do Itabapoana (21°18′S), in the state of Rio de Janeiro, namely northern distributional gap (Gap I); and (2) from Macaé (22°25′S) to Ilha Grande (23°09′S), in Rio de Janeiro, namely southern distributional gap (Gap II) (e.g. Azevedo et al., 2002; Danilewicz et al., 2012; de Moura et al., 2009). Systematic and long-term monitoring has confirmed the absence of franciscanas, mainly in the central portion of these gaps (e.g. de Moura et al., 2009). However, there is no consensus about the exact boundaries of the gaps (e.g. Azevedo et al., 2002; Siciliano et al., 2015) which play an important role in the delineation of management units for the species (Secchi et al., 2003a).

Previous studies revealed the existence of geographical population structure based on external morphology and genetic markers (e.g. Higa et al., 2002; Ott, 2002; Pinedo, 1995; Ramos et al., 2002; Secchi et al., 1998). After applying a multi-methodological approach for identifying

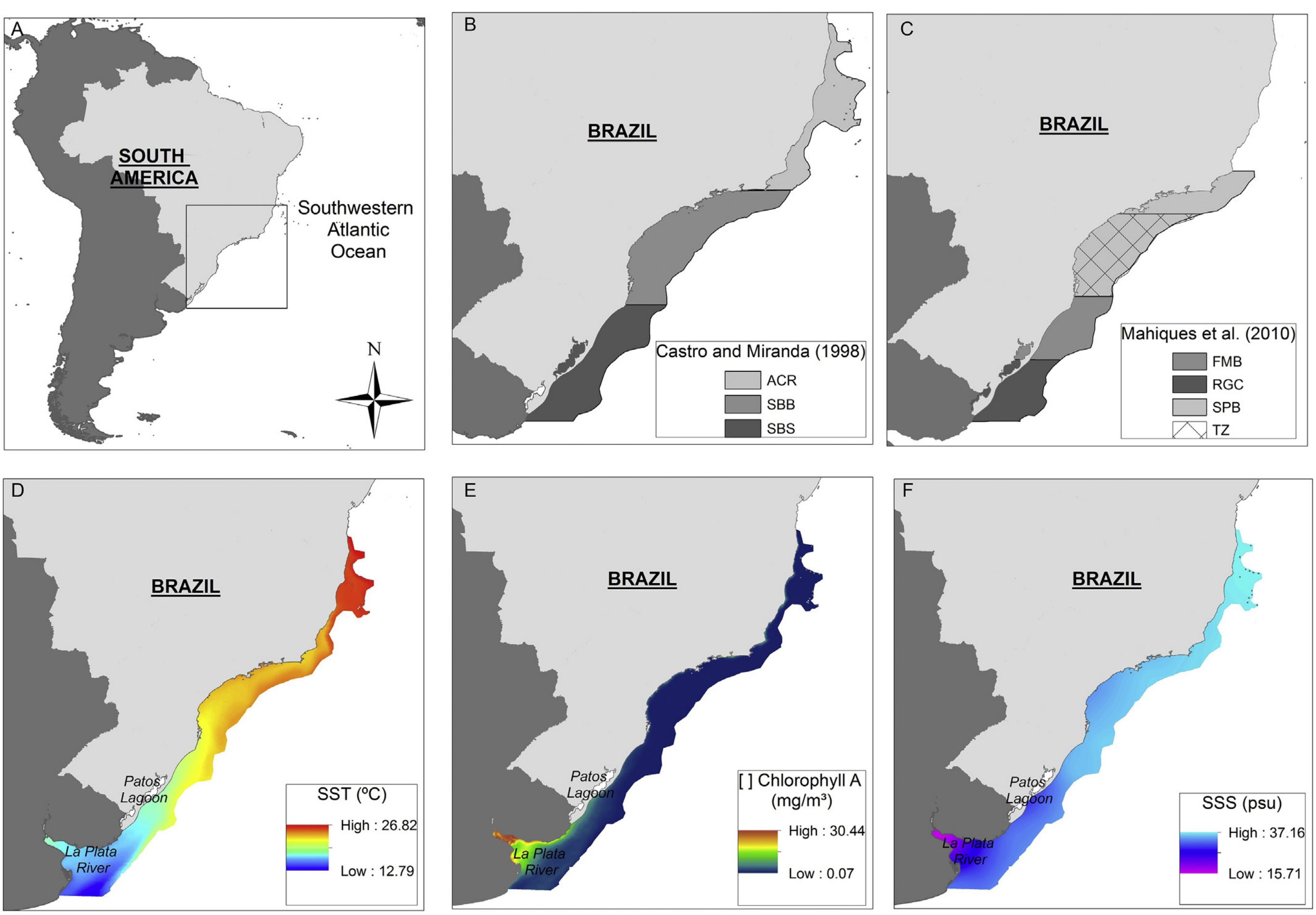

Fig. 1. A) Study area of franciscana dolphin distribution. Brazilian continental shelf zones proposed by B) Castro and Miranda (1998) and C) Mahiques et al. (2010). Representation of annual means of D) Mean Annual Sea Surface Temperature (SST), E) Mean Annual Concentration of Chlorophyll A, and F) Mean Annual Sea Surface Salinity (SSS). Abbreviations: ACR, Abrolhos – Campos Region; SBB, South Brazilian Bight; SBS, Southern Brazilian Shelf; SPB, São Paulo Bight; FMB, Florianópolis – Mostardas Bight (FMB); RGC, Rio Grande Cone; TZ, Transitional Zone.

stock discreteness, Secchi et al. (2003a) divided the franciscana's range into four Franciscana Management Areas (FMAs) (please see Fig. 1 of the refereed article). FMA I and FMA II are located exclusively in southeastern and southern Brazil, FMA III includes southern Brazil and Uruguay, and FMA IV encompasses the range of the species in Argentina. These management divisions are supported by recent data on pollutant loads, diet, external morphology and parasites (e.g. Alonso et al., 2012; Barbato et al., 2012; Costa-Urrutia et al., 2012; de la Torre et al., 2012; Hoss et al., 2017). New studies have suggested the need of reformulation of the former FMA's subdivisions (e.g. Gariboldi et al., 2015, 2016; Mendez et al., 2010), including the separation of FMA I in two distinct management units (FMA Ia and FMA Ib) separated by the northern distributional gap (Anonymous, 2015; Cunha et al., 2014).

The increased effort from properly designed aerial surveys to estimate franciscana's abundance (e.g. Danilewicz et al., 2010, 2012; Zerbini et al., 2011) and long-term projects evaluating franciscana bycatch (see Material and Methods) have provided many georeferenced at-sea records for the species. These data have been useful to characterise the distributional ecology of franciscanas' populations in a comprehensive manner and can be used to perform ecological niche modeling in order to investigate factors that influence their distribution.

Correlative species distribution models are based on algorithms that estimate ecological niches and explore potential distributional areas by assessing relationships between species occurrences and environmental information (Qiao et al., 2016). Niche modeling approaches dramatically expanded in recent years and currently several techniques and toolkits are available (Phillips et al., 2006; Qiao et al., 2016). In addition, these techniques have been widely used in studies on the distribution of cetaceans (e.g. do Amaral et al., 2015; Palacios et al., 2013; Rossi-Santos and Oliveira, 2016), including estimates of the potential franciscana distribution (Gomez and Cassini, 2015).

Given the high risk faced by the franciscana, especially the extremely high risk of extinction observed regionally in Brazil (Rocha-Campo et al., 2010), and the importance of distributional ecology to either the process of risk assessment and conservation planning, the aim of this study is (1) to update information on the franciscana distribution in Brazil, including a review of FMAs I, II and III as well as the distributional gaps between them, and (2) to investigate the factors that potentially explain the existence of gaps in the range of the franciscana.

2. Materials and methods

2.1. Study area

The study area includes the Brazilian continental shelf from 18°S to 34°S, including only those waters up to the 50 m isobath (Fig. 1A). The area is characterized by different physical oceanographic processes. Castro and Miranda (1998) therefore proposed a segmentation of the Brazilian continental shelf into six zones, of which three zones are encompassed by the study area: Abrolhos – Campos Region (15°S – 23°S), South Brazilian Bight (23°S – 28°30′S) and Southern Brazilian Shelf (28°30′S – 34°S) (Fig. 1B). These areas are characterized by different features in relation to topography, productivity, sea surface temperatures and salinity due to upwelling, land runoff from several estuaries and convergence of currents (Fig. 1D–F). Conversely to Castro and Miranda (1998), who proposed a division of the Brazilian continental shelf for practical reasons, Mahiques et al. (2010) suggest a division in terms of geology, bathymetry, declivities and the presence of canyons and channels (Fig. 1C).

2.2. Franciscana dataset

Franciscana records used in the present analyses corresponded to observations of live animals in situ through dedicated aerial and boat surveys or to specimen entangled in coastal gillnets fisheries in Brazil (for which precise location data were available). Only data from the marine environment were considered, therefore franciscana records previously observed in estuarine areas such as Babitonga Bay (Cremer and Simões-Lopes, 2005, 2008) and Paranaguá Bay (Santos et al., 2009) in southern Brazil were not included. Only sightings data from dedicated surveys and georeferenced data from bycatch were used in the present analysis in order to estimate franciscana's fundamental ecological niche. Sampling effort and potential biases associated with non-uniform sampling effort, especially those related to fishery monitoring, have not been considered in this study.

Data from aerial surveys were obtained through dedicated line transect studies designed to assess franciscana distribution and to estimate abundance (details in Danilewicz et al., 2010, 2012; Zerbini et al., 2011). Bycatch data were obtained directly by some of the authors via onboard surveys or logbook information provided by reliable and well known captains of fishing vessels operating along the Brazilian coast from 1992 to 2004 (Danilewicz, 2007; Danilewicz et al., 2009; Ott, 1998; Secchi et al., 1997, 2004). Additional records were obtained from peer-reviewed literature (Di Beneditto, 2003; Di Beneditto et al., 2001; Flores, 2009; Moreno et al., 2003; Santos and Netto, 2005; Santos et al., 2002, 2009; Siciliano et al., 2002).

2.3. Environmental dataset

Ten environmental variables that are considered to influence cetaceans distributions (e.g. Baumgartner et al., 2001; Palacios et al., 2013; Redfern et al., 2006) and specifically franciscanas (Gomez and Cassini, 2015; Siciliano et al., 2002) were initially selected to describe the characteristics of the franciscana's habitats and distributional gaps (Table 1).

Environmental information was obtained from Bio-Oracle (Tyberghein et al., 2012) and MARSPEC (Sbrocco and Barber, 2013). These public databases provide a set of user-friendly and high-resolution GIS data layers of the ocean and were designed for species distribution modeling applications (Sbrocco and Barber, 2013; Tyberghein et al., 2012). The layers consist of global coverage satellite-based and in situ measured data interpolated and assembled at an annual temporal resolution and at different spatial resolutions (1 km and 9 km from MARSPEC and Bio-Oracle datasets, respectively). Geophysical layers were derived from the SRTM30_PLUS high resolution bathymetry dataset (Sbrocco and Barber, 2013), and bioclimatic layers were derived from a long term dataset from NOAA's World Ocean Atlas and NASA's MODIS satellite imagery (Sbrocco and Barber, 2013; Tyberghein et al., 2012; for more details about environmental dataset access: http://www.marspec.org/ and http://www.oracle.ugent.be/). All environmental layers were processed in ArcGIS 10.2.2 (ESRI, 2013) in datum WGS 84, using the same spatial extent (18°S

Table 1
List of environmental variables analyzed in this study and its respective source, resolution and unit.

Environmental variables	Source	Unit	Original resolution
Bathymetry (Depth of the seafloor)	MARSPEC	Meters	1 km
Distance to shore	MARSPEC	Kilometres	1 km
Bathymetric Slope	MARSPEC	Degrees	1 km
Mean Annual Concentration of Chlorophyll A	Bio-Oracle	mg/m^3	9 km
Annual Range in Concentration of Chlorophyll A	Bio-Oracle	mg/m^3	9 km
Mean Annual Diffuse Attenuation	Bio-Oracle	m^{-1}	9 km
Mean Annual Sea Surface Salinity	MARSPEC	Psu	1 km
Annual Range in Sea Surface Salinity	MARSPEC	Psu	1 km
Mean Annual Sea Surface Temperature	MARSPEC	degrees °C	1 km
Annual Range in Sea Surface Temperature	MARSPEC	degrees °C	1 km

to 34°S) at a 9 km resolution.

In order to assess the shelf habitat available for franciscanas in the study area, distance to shore data was obtained from distance to shore layer, in which we extracted its values at 0.5° latitudinal intervals along the 25 m and 50 m isobaths.

2.4. Environmental analyses

Non-independence of predictor variables is a well-known problem in ecology (e.g. Dormann et al., 2013), and it is recommended a preliminary selection of layers in order to avoid redundant data layers in ecological niche analysis (e.g. Qiao et al., 2016). Therefore, correlation of environmental layers was assessed, and factorial analyses were used to select variables with low multicollinearity. Collinearity analyses were conducted in R Statistical Software version 3.2.4 (R Development Core Team, 2016) using the corrplot package (Wei and Simko, 2016) on all variables presented in Table 1, with the exception of distance to shore.

Non-parametric tests (Kruskal-Wallis and Dunn tests) were conducted to provide a preliminary assessment of potential differences between occupied and unoccupied areas with respect to environmental variables selected by the factorial analysis. In order to comply with the assumptions of independence and randomization of sampling required by nonparametric tests, sample points randomly distributed throughout the study areas were used. In a first step, polygons were designed representing areas adjacent to the gaps (i.e. FMA Ia, FMA Ib and FMA II) and areas not occupied by franciscana (i.e. gaps). The polygons were constrained longitudinally by the 50 m isobath, and latitudinally by the limits for the new FMAs proposed here (see Results section). In a second step, a number of random points within each polygon were generated taking into account the proportions of areas (100 points were created within the polygon with the smallest area and so forth). Data were then grouped as "Area occupied by Franciscana (AOF)", Gap I, and Gap II. AOF corresponded to the region between Itaúnas in Espírito Santo, and the center of Ilha de Santa Catarina in the state of Santa Catarina, without a discrimination of FMAs and the exclusion of distributional gaps. Finally, significant differences were tested among the medians of the variables identified by the factorial analysis using a Kruskal-Wallis test followed by the Dunn test. All statistical tests were performed in software R Statistical Software version 3.2.4 (R Development Core Team, 2016) using the nortest (Gross and Ligges, 2015) and the dunn (Dinno, 2017) packages. A significance level of $\alpha = 0.05$ was adopted and the *p*-value for multiple comparisons was adjusted using the Bonferroni method.

2.5. Ecological niche analysis

NicheA 3.0 (Qiao et al., 2016) was used to investigate if the distributional gaps are consistent with franciscana's fundamental ecological niche. NicheA software generates ecological niche models following the Hutchinsonian approach of an n-multidimensional space, and projects these models in geographic space in the form of continuous species suitability models (for details, see Qiao et al., 2016). NicheA assumes that a species' fundamental ecological is convex in shape, and thus can be operationalized as minimum-volume ellipsoids (MVE) (Qiao et al., 2016). Similar to others modeling approaches (e.g. Maxent – Phillips et al., 2006), MVE could be influenced by sampling biases; however, MVE is only influenced by bias in the periphery of the cloud points. If there are sampling biases that affect the concentrations of points in the interior of the cloud, those will have no effect (A. Townsend Peterson 2017, personal

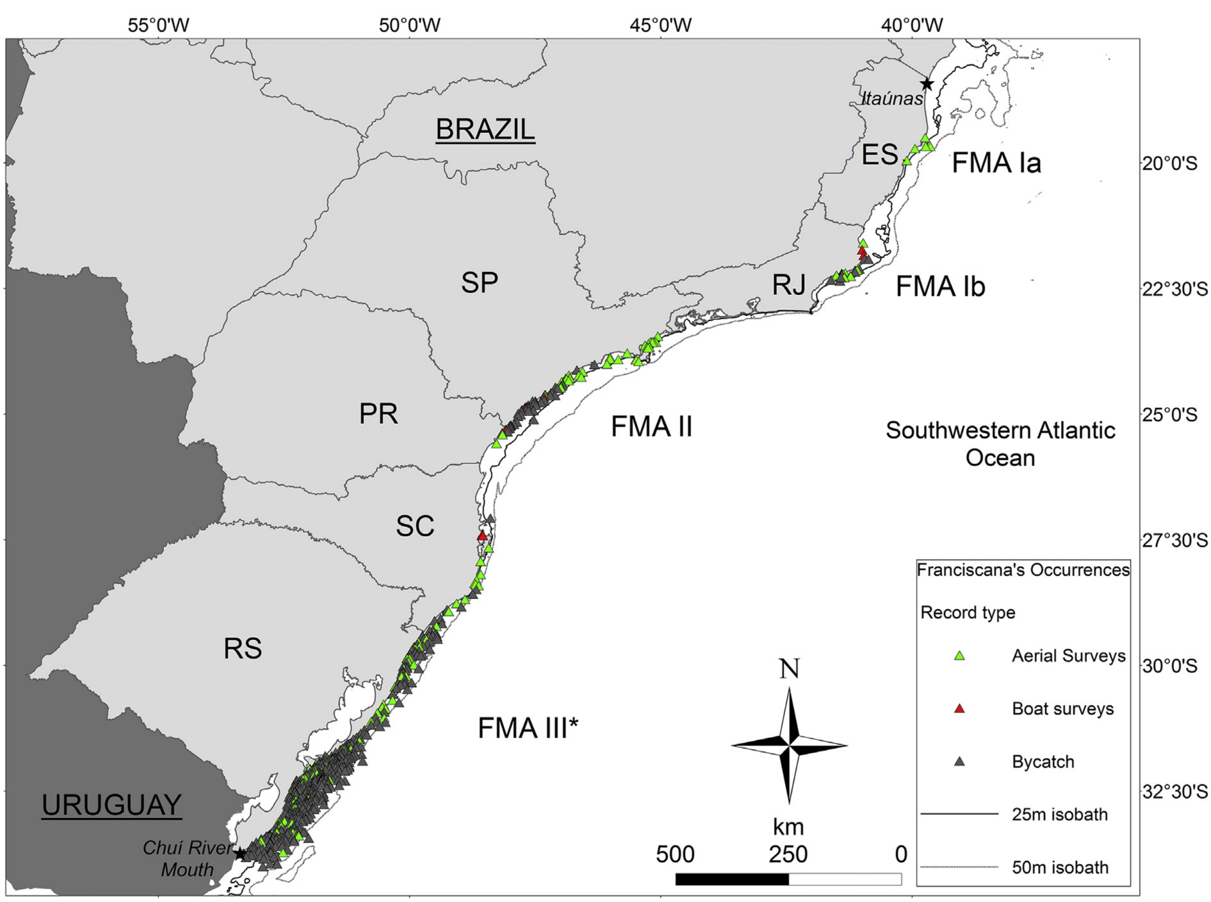

Fig. 2. Compiled records of franciscana dolphin along Brazilian coastal waters from Itaúnas (ES) to Chuí River Mouth (RS). Abbreviations: ES, Espírito Santo; RJ, Rio de Janeiro; SP, São Paulo; PR, Paraná; SC, Santa Catarina; RS, Rio Grande do Sul.

communication). This means that MVE is not influenced by the density of the points (Huiji Qiao 2017, personal communication). Considering the biased nature of the franciscana data set (e.g. uncorrected for effort), NicheA was deemed the most suitable tool to investigate the characteristics of the franciscana's distribution. In order to better represent the franciscana's fundamental niche, all types of records (bycatch, aerial and boats surveys) were pooled.

Finally, MVEs, representing the franciscanas' fundamental ecological niche, were projected to a habitat suitability map. For the MVE, continuous values of suitability were assessed as the Euclidean distance to the niche centroid (Qiao et al., 2016). The most suitable areas are those closest to the niche centroid (with values close to 1), while the most unsuitable are those areas further away from the niche centroid (with values close to 0); areas totally outside of species niche were set to −1 suitability.

3. Results

3.1. Franciscana distribution update

In total, 788 records of franciscanas in Brazil were compiled from Itaúnas (18°25′S) in Espírito Santo to Chuí River Mouth (33°44′S) in the state of Rio Grande do Sul, located on the Brazil-Uruguay border (Fig. 2). Most of the data were collected between 1992 and 2014. Bycatch data represented 78% of these records, sightings from aerial surveys represented 20.9% and sightings from boat surveys accounted for only 1.1% of the overall data (records for each FMA are summarized in Table 2).

Based on the records compiled, a reassessment of the limits of the FMAs and the distributional gaps were proposed (Table 2, Fig. 3). The distributional gaps were defined as following: Gap I is located from Santa Cruz (19°57′S) to Barra de Itabapoana (21°18′S) in Espírito Santo; Gap II is located from Armação dos Búzios (22°44′S) to Piraquara de Dentro (22°59′S) in Rio de Janeiro.

3.2. Environmental layers analyses

From nine layers initially considered to have some influence in the franciscana's distribution, four pairs of environmental layers exhibited correlation coefficient higher than 0.7 (Fig. 4). Therefore, the following environmental layers were selected based on the highest value of each factor of factorial analyses (Table 3): Mean Annual Diffuse Attenuation, Annual Range in Sea Surface Temperature, Mean Annual Sea Surface Salinity, and Bathymetry.

Polygons representing areas adjacent to the gaps (i.e. FMA Ia, FMA Ib and FMA II) and areas not occupied by franciscana (i.e. gaps) are presented in Fig. 5. Considering the proportions of areas, the number of random points created for each polygon is presented in Table 4.

Differences between AOF and Gap I were statistically significant for Mean Annual Sea Surface Salinity (Tables 5 and 6, Fig. 6A), and Annual Range in Sea Surface Temperature (Tables 5 and 6, Fig. 6B). Differences between AOF and Gap II were statistically significant for Annual Range in Sea Surface Temperature (Tables 5 and 6, Fig. 6B) and Mean Annual Diffuse Attenuation (Tables 5 and 6, Fig. 6C). Gap I and Gap II were statistically differentiated in relation to Mean Annual of Sea Surface Salinity (Tables 5 and 6, Fig. 6A), Annual Range in Sea Surface Temperature (Tables 5 and 6, Fig. 6B) and Mean Annual of Diffuse Attenuation (Tables 5 and 6, Fig. 6C). Bathymetry was not statistically different among the areas analyzed (Table 5, Fig. 6D). In general, Gap I had the highest median of Mean Annual of Sea Surface Salinity; Gap II had the highest median of Mean Annual of Diffuse Attenuation; and, AOF had the highest median of Annual Range in Sea Surface Temperature.

3.3. Ecological niche analysis

The franciscana's Minimum-Volume Ellipsoid (MVE, representing the franciscana's fundamental ecological niche) was estimated using 788 occurrence records in a three-dimensional environmental space represented by Mean Annual Diffuse Attenuation, Annual Range in Sea Surface Temperature, Mean Annual Sea Surface Salinity, and Bathymetry in NicheA.

The franciscana's distribution model (i.e. the MVE projected in geographic space) revealed that the waters in the continental shelf up to 25 m were closest to niche centroid (values close to 1), therefore these areas corresponded to the most suitable habitat for franciscanas (Fig. 7). On the other hand, water depths between 25 m and 50 m isobaths exhibited a progressive decrease of environmental suitability and were more distant from franciscana niche centroids (values close to 0). Gap I and Gap II exhibited values of distance to niche centroid lower than 0.75.

3.4. Shelf habitat availability

The 25 m isobath was very close to the shore in the areas corresponding to distributional gaps (i.e. very little area with shallow waters), while the areas suitable for franciscanas were characterized by shallow waters (up to the 50 m isobath) up to quite some distance from the coast. In the Gap I, 25 m isobaths were identified between 5 km and 30 km of coastal line. In the Gap II, the 25 m isobaths were at < 10 km from shore, as close as just 1 km from the coast line at 23°S (close to Arraial do Cabo in Rio de Janeiro; see Fig. 8).

The location of the 50 m isobath was similar to those of 25 m, being closest to shore in the areas corresponding to the gaps. In the Gap I, 50 m isobaths was > 30 km far from coast line. In the Gap II, 50 m isobaths was positioned closest to shore, being < 1 km far from shore at 23°S (Fig. 8). In addition to the distributional gaps, a marked narrowing of continental shelf is also observed around the Ilha de Santa Catarina (27°35′S) (Fig. 8).

Table 2
Summary of franciscanas' records by areas and data source and gaps limits. FMAs were established according to Cunha et al. (2014) and limits were updated.

Records summary information					
Areas	New limits	Aerial Surveys	Boat Surveys	Bycatch	Total
FMA Ia	Itaúnas, ES (18°25′S) to Santa Cruz, ES (19°57′S)	6	0	0	6
Gap I (north)	Piraquê-Açu River Mouth, Santa Cruz, ES (19°57′S) to Barra de Itabapoana, ES (21°18′S)				
FMA Ib	Barra de Itabapoana, RJ (21°18′S) to Armação de Búzios, RJ (22°44′S)	13	2	11	26
Gap II (south)	Armação dos Búzios, RJ (22°44′S) to Piraquara de Dentro, RJ (22°59′S)				
FMA II	Piraquara de Dentro, RJ (22°59′S) to Ilha de Santa Catarina, SC (27°35′S)	41	7	60	108
FMA III[a]	Ilha de Santa Catarina, SC (27°35′S) to Chuí River Mouth, RS (33°44′S)	105	0	543	648
TOTAL		165	9	614	788
Percentage (%)		20.9%	1.1%	78.0%	100.0%

Abbreviations: ES, Espírito Santo; RJ, Rio de Janeiro; SC, Santa Catarina; RS, Rio Grande do Sul.
[a] FMA III is partially represented, because it extends into Uruguay.

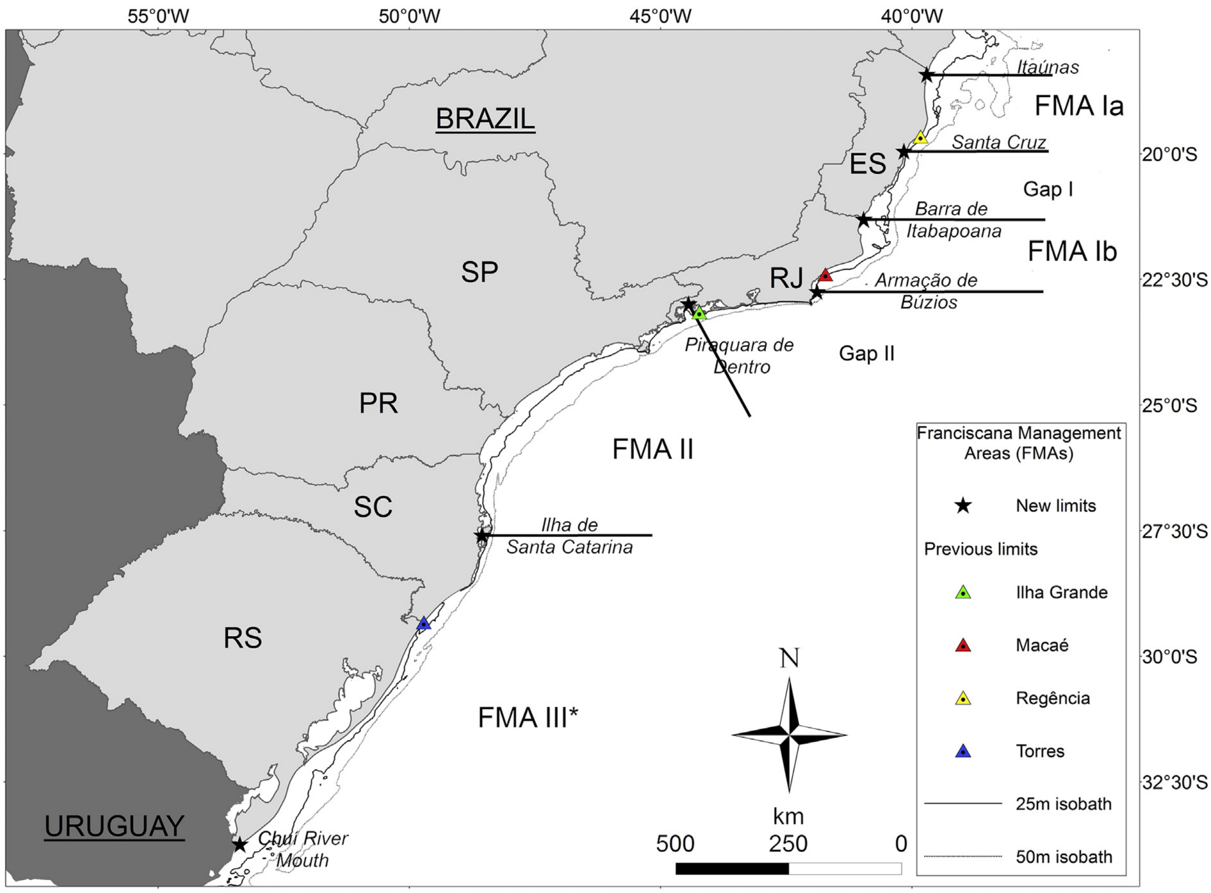

Fig. 3. New geographic ranges of the Franciscanas Management Areas (FMAs) and distributional gaps. Localities already considered limits are indicated in the map by triangles symbols. Abbreviations: ES, Espírito Santo; RJ, Rio de Janeiro; SP, São Paulo; PR, Paraná; SC, Santa Catarina; RS, Rio Grande do Sul. *FMAIII is partially represented because this management area extends further to the south to include the coast of Uruguay.

4. Discussion

The comprehensive review of the franciscana's occurrences along Brazilian coastal waters support the boundaries of FMAs as well as distributional gaps proposed by franciscanas' experts recently (see Anonymous, 2015; Ott et al., 2015). In relation to previous studies (for instance Secchi et al., 2003a; Siciliano et al., 2002), FMA Ia was extended further south from Regência (19°40′S) to Santa Cruz (19°57′S) in Espírito Santo; the southern limit of FMA Ib was relocated southward from Macaé (22°25′S) to Armação de Búzios (22°44′S) in Rio de Janeiro, due to the stranding of a live animal in the locality of Manguinhos, Armação de Búzios, reported by Siciliano et al. (2015). The northern limit of FMA II was established as Piraquara de Dentro (22°59′S) in Rio de Janeiro, while the southern limit was dislocated further northward from Torres (29°20′S) to the center of Ilha de Santa Catarina (27°35′S) in Santa Catarina, based on previous genetic studies (Cunha et al., 2014; Ott, 2002) (see Fig. 3). These changes on FMAs have impact direct on the extension of distributional gaps, which by its turn were reduced in relation to previous studies (Azevedo et al., 2002; Danilewicz et al., 2012; de Moura et al., 2009; Secchi et al., 2003a; Siciliano et al., 2002).

In general, the habitat suitability model presented here confirmed the well-known distribution of franciscanas (Danilewicz et al., 2009), indicating high environmental suitability for the species mainly up to the 25 m isobath (Fig. 7). However, this highly suitable environment could extend up to 50 m in the southernmost portion of franciscanas' distribution in Brazil as already indicated by Danilewicz et al. (2009). The ecological niche analyses also showed that both distributional gaps seem suitable for franciscanas at some level and they are inside of the fundamental niche of species.

The resulting map of environmental suitability generated here is consistent with that proposed by Gomez and Cassini (2015), where habitat suitability map indicated high suitability for franciscanas in waters up to approximately 30 m depth from Brazil to Argentina (Gomez and Cassini, 2015). Even though Gomez and Cassini (2015) did not include bathymetry as a predictor, their resulting map agreed with the IUCN map. On the other hand, the franciscana's IUCN map was proposed by experts based on the 30 m isobath to establish the eastern border of franciscanas' distribution. In contrast to Gomez and Cassini (2015), the habitat suitability model proposed here indicated some level of suitability for franciscana in the gaps.

Bathymetry and distance to shore are considered important predictors of franciscanas' distribution (e.g. Danilewicz et al., 2009; Secchi and Ott, 1999), since individuals are rarely recorded beyond 50 m isobaths (Danilewicz et al., 2009). However, the present analysis did not indicate that bathymetry differs statistically among the area occupied by franciscanas and the gaps (Fig. 6D). On the other hand, the analysis of shelf habitat availability indeed revealed that the continental platform is extremely narrow in the gaps, reaching just 1 km of distance from shore at 23°S, for instance (Fig. 8). It was already suggested the narrowing of the continental shelf in the distributional gaps would limit habitat availability for franciscanas (Di Beneditto et al., 2001; Netto and Siciliano, 2007; Siciliano et al., 2002).

A similar example has been demonstrated in the western South Atlantic with the Atlantic spotted dolphin *Stenella frontalis* (G. Cuvier 1829). A gap in the distribution of this dolphin species exists where the Brazilian continental shelf narrows substantially between Abrolhos Bank (~18°S) and 6°S (Danilewicz et al., 2013; Moreno et al., 2005).

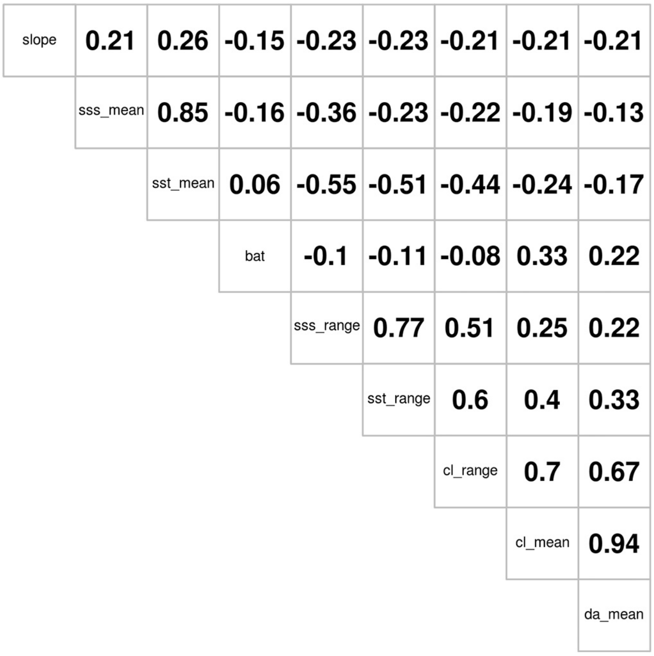

Fig. 4. Correlation matrix of nine environmental variables evaluated in the study. Abbreviations: bat, Bathymetry; slope, Bathymetric Slope; da_mean, Mean Annual Diffuse Attenuation; cl_mean, Mean Annual Concentration of Chlorophyll A; cl_rg, Annual Range in Concentration of Chlorophyll A; sss_mean, Mean Annual Sea Surface Salinity; sss_range, Annual Range in Sea Surface Salinity; sst_mean, Mean Annual Sea Surface Temperature; sst_range, Annual Range in Sea Surface Temperature.

Ecological niche modeling revealed lack of optimal environmental conditions for the species in the region of the coast where the continental shelf narrows (see do Amaral et al., 2015). In relation to franciscanas' distribution it is also interesting to note that a narrowing of continental shelf also exists around Ilha de Santa Catarina (27°35'S), where the limits between the FMA II and FMA III has been proposed (Ott, 2002; Cunha et al., 2014).

Analysis performed here showed that Gap II is located in a very restrict band of continental shelf, where the coastline orientation changes abruptly from NE-SW to E-W (Castro and Miranda, 1998). The continental shelf is almost nonexistent in the Gap II resulting in a drastic reduction of the shelf habitat even if other conditions such as temperature, salinity and productivity could support the existence of species. In relation to Gap I, for example, the narrow shelf associated with higher levels of salinity could play a role to explain the absence of franciscanas in this area.

Table 3
Factorial analysis of nine environmental variables used in this study.

	Factor1	Factor2	Factor3	Factor4	Factor5
bat	0.135			0.771	
slope	−0.143	−0.226	0.155		0.126
cl_mean	0.929	0.190		0.289	
cl_range	0.695	0.440	−0.169	−0.190	0.163
da_mean	0.959	0.122		0.128	−0.208
sss_mean		−0.121	0.976	−0.147	
sss_range	0.118	0.791	−0.271		
sst_mean	−0.123	−0.404	0.837	0.102	
sst_range	0.256	0.884	−0.129		
SS loadings	2.402	1.887	1.805	0.786	0.104
Proportion Var	0.267	0.210	0.201	0.087	0.012
Cumulative Var	0.267	0.477	0.677	0.765	0.776

Abbreviations: bat, Bathymetry; dist, Distance to Shore; slope, Bathymetric Slope; da_mean, Mean Annual Diffuse Attenuation; cl_mean, Mean Annual Concentration of Chlorophyll A; cl_range, Annual Mean in Concentration of Chlorophyll A; sss_mean, Mean Annual Sea Surface Salinity; sss_range, Annual Range in Sea Surface Salinity; sst_mean, Mean Annual Sea Surface Temperature; sst_range, Annual Range in Sea Surface Temperature.

As suitability was projected in the distributional gaps, the absence of franciscana could be attributed to the reduction in the shelf habitat due to the narrowing of continental shelf. This environmental change could in turn intensify the biotic interactions such as competition by food and predation with other marine species. Guiana dolphin *Sotalia guianensis* (Van Bénedén, 1864) is a species with similar habitats (Da Silva et al., 2010) and could compete with franciscana by food and/or space. Furthermore, it was already observed a significant overlap in the diet of franciscana and largehead hairtail *Trichiurus lepturus* Linnaeus, 1758 (see Bittar and Di Beneditto, 2009; Di Beneditto et al., 2013). Also, the reduction of shelf habitat could enhance the vulnerability to predation by other cetaceans such as killer whale *Orcinus orca* (Linnaeus, 1758) (e.g. Ott and Danilewicz, 1998; Santos and Netto, 2005). Besides the likely strengthening of these biotic interactions, intrinsic factors, as minimal viable population size, also can play an important role in this very reduced range of habitat. In fact, a synergistic effect of biotic and abiotic factors can be determinant for the absence of franciscanas in the distributional gaps.

As top predators, cetacean distribution is limited by different factors (for example, productivity, temperature and salinity) that constraint both its prey and predator's distributions (e.g. Baumgartner et al., 2001; Palacios et al., 2013; Redfern et al., 2006). Temperature is a well-recognised factor delimiting species distribution (e.g. Jeffree and Jeffree, 1994) and salinity is also a well-known factor that have influence on cetacean distribution due to importance of physiological mechanisms to maintain the water and salt balance in cetaceans (e.g. Xu et al., 2013). Therefore, both salinity and temperature seem to impose physiological constraints for franciscanas, including stress triggered by high salt levels (e.g. São Pedro et al., 2015; Xu et al., 2013) and offspring resistance to cold environment (e.g. Danilewicz, 2003).

The presence of franciscana in FMA Ia appears to be associated with the plume of Doce River that probably maintains the levels of salinity more favorable to franciscanas or its prey species (Netto and Siciliano, 2007; Siciliano et al., 2002). Therefore, higher levels of salinity in Gap I could be a potential explanation for the absence of franciscanas in this area, once this gap has the highest median of Sea Surface Salinity. Since the franciscana seems to be associated with areas with great salinity ranges such as estuaries or river mouths (Cremer and Simões-Lopes, 2005; Santos et al., 2009; Siciliano et al., 2002), a higher constant salinity could impose some physiological constraint to the franciscana and/or to its prey species. Although franciscana has a fairly opportunist behavior in terms of prey abundance and occurrence (Bassoi, 2005) and shifts in prey composition overtime were already detected in southern Brazil (Secchi et al., 2003b), sciaenid fishes and long-finned squid *Doryteuthis sanpaulensis* (Brakoniecki, 1984) are very representative in the diet of the franciscana along its geographic range (Bassoi, 2005; Danilewicz et al., 2002). Sciaenid species are mainly present in tropical to warm and temperate environments over sandy and muddy bottoms in brackish, estuarine and low-salinity coastal regions (Martins and Haimovici, 2016).

Gomez and Cassini (2015) also suggested based on their ecological niche analysis that temperature and salinity could be considered the environmental predictors of franciscana along its entire range as well as the potential distribution of the stripped weakfish *Cynoscion guatucupa* (Cuvier, 1830). They also highlighted the physiological constrains imposed by Sea Surface Temperature and Salinity, and they did not find any support for previous statements that turbidity could be an important ocean determinant of franciscana distribution.

Diffuse attenuation is an indicator of the water turbidity and it is directly related to the presence of scattering particles in the water column. The analysis performed here indicated that the Gap II has the highest median of Diffuse Attenuation. This finding is a little bit controversial in relation to previous studies that suggested a preference for

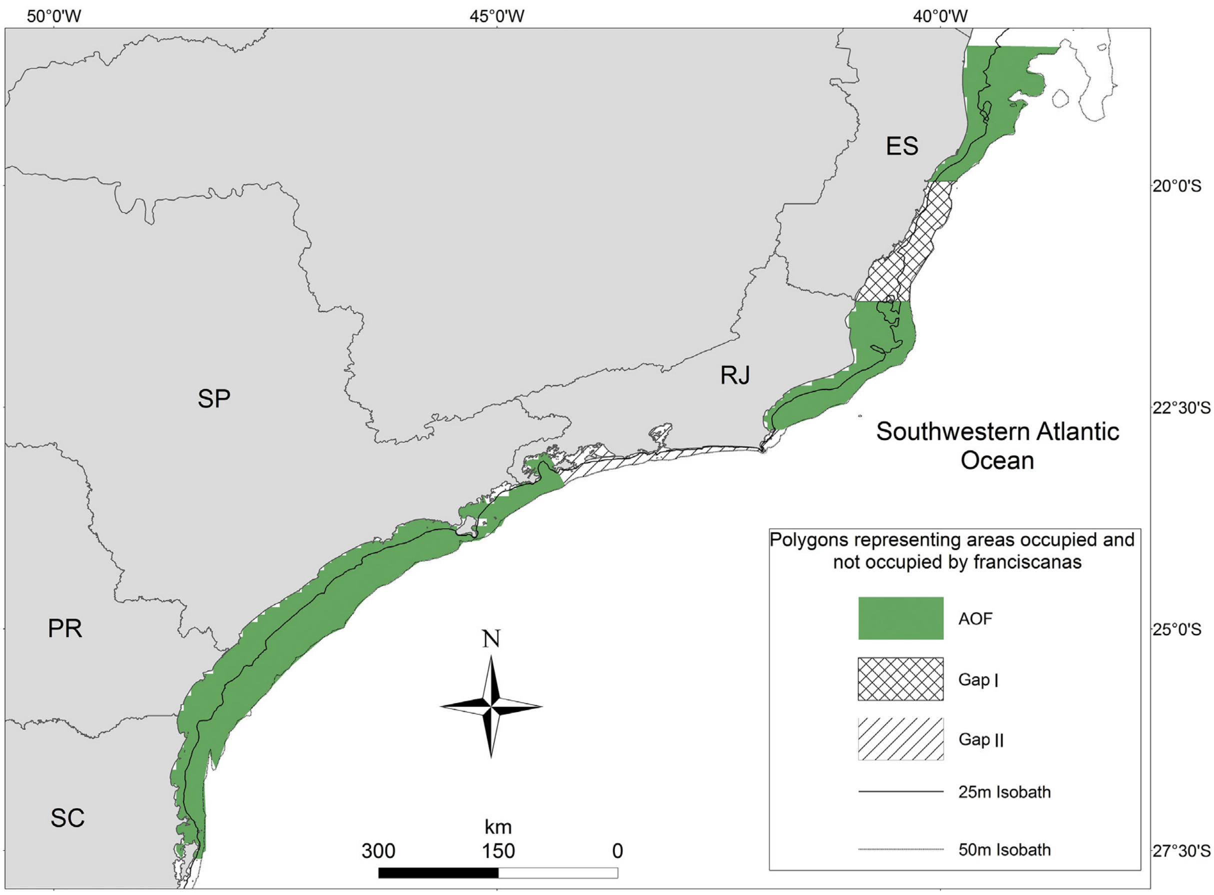

Fig. 5. Map of polygons used to create random points in order to represent the area occupied by franciscana and those not occupied. Abbreviation: AOF, Area occupied by Franciscana.

Table 4
Information used to investigate the environmental distinctiveness of areas occupied and not occupied by franciscanas. Abbreviation: AOF, Area Occupied by Franciscana.

Areas		Proportion in relation to the smallest polygon (i.e., Gap II)	Number of random points generated
AOF	Area Ia	2.44	244
	Area Ib	2.34	234
	Area II	7.72	772
Gap I		1.48	148
Gap II		1	100

Table 5
Medians comparisons through Kruskal-Wallis.

Environmental layer	Kruskal-Wallis Test	
Mean Annual Sea Surface Salinity	**χ2 = 106.45**	***p*-value < .05**
Annual Range in Sea Surface Temperature	**χ2 = 164.01**	***p*-value < .05**
Mean Annual Diffuse Attenuation	**χ2 = 19.799**	**p-value < .05**
Bathymetry	χ2 = 4.0115	p-value =.13

Statistically significant values are in bold.

Table 6
Areas medians comparisons through Dunn tests for each environmental layer, which Kruskal -Wallis test was significant.

Dunn test			
	AOF	Gap I	
Mean Annual Sea Surface Salinity	**−10.229 (0.00001)**	–	Gap I
	0.433967 (0.9965)	7.218 (0.00001)	Gap II
Annual Range in Sea Surface Temperature	**12.13 (0.00001)**	–	Gap I
	5.165059 (0.00001)	**−3.999 (0.0001)**	Gap II
Mean Annual Diffuse Attenuation	−0.664 (0.7597)	–	Gap I
	−4.441 (0.00001)	**−3.119 (0.0027)**	Gap II

Abbreviation: AOF, Area Occupied by Franciscana. P-value is indicated among parenthesis and statistically significant values are in bold.

turbid waters by franciscanas (Siciliano et al., 2002). The reader should be aware that these results are influenced by the Guanabara Bay, Rio de Janeiro, and its discharge, which in turn could be increasing the values of Diffuse Attenuation, not reflecting a condition along the entire Gap II.

Finally, it is important to highlight that distributional gaps have an immediate impact on the population structure of franciscanas mainly in relation to franciscanas from FMA I. Genetic evidences based on mtDNA suggests that franciscanas are divided in two evolutionary lineages, franciscanas from FMA I (i.e. those northward Gap II) being a distinct lineage in comparison to all remaining franciscanas (Cunha et al., 2014). Furthermore, FMA I is further sub-structured into FMA Ia and FMA Ib (Cunha et al., 2014). From these findings it is possible to assume that both northern and southern distributional gaps have been acting as a barrier long enough to have an impact on the population structure in the areas adjacent to the gaps. Considering the importance of shelf habitat for franciscanas, it seems to be reasonable to suppose that historical factors such as sea level oscillations and, consequently, fragmentation of coastal platform during glacial and interglacial cycles,

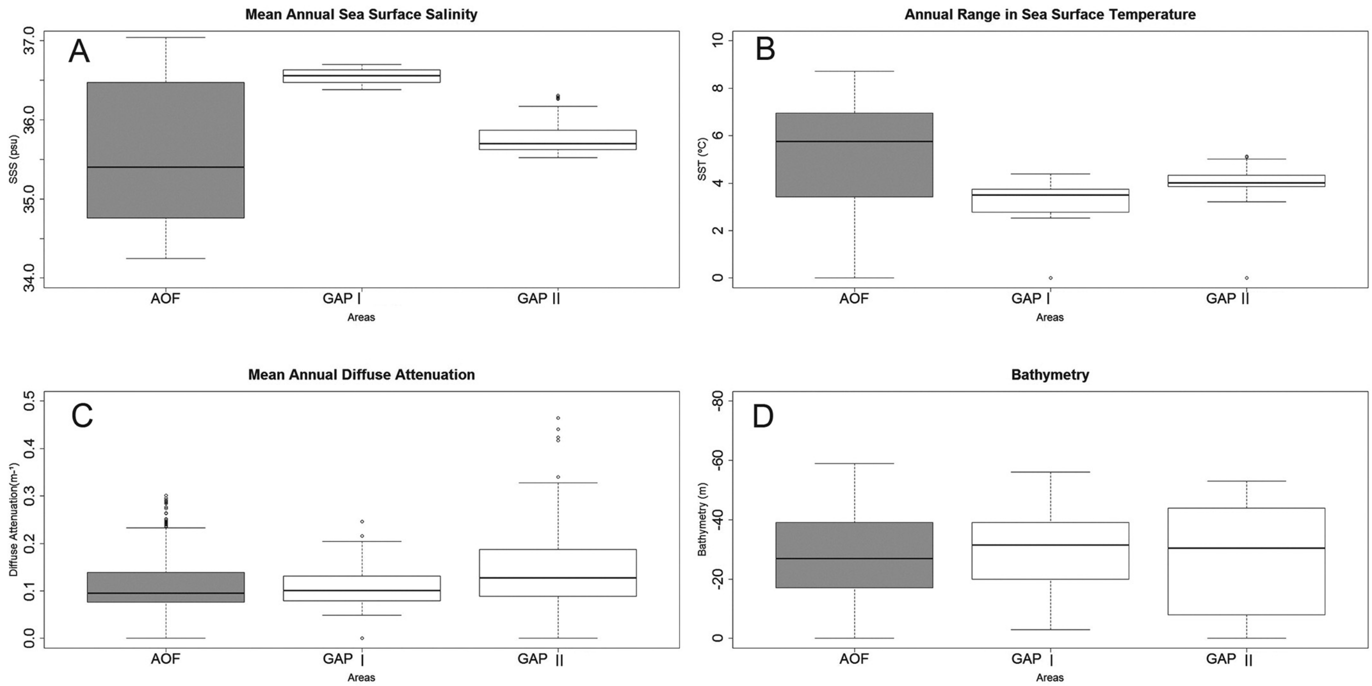

Fig. 6. Boxplot of environmental values extracted from random points grouped according area occupied by franciscana (AOF) and those not occupied. Boxplot represents median, 25th and 75th percentiles, and 5th and 95th are represented by the errors bars. In A) Mean Annual Sea Surface Salinity; B) Annual Range in Sea Surface Temperature; C) Mean Annual of Diffuse Attenuation; and D) Bathymetry.

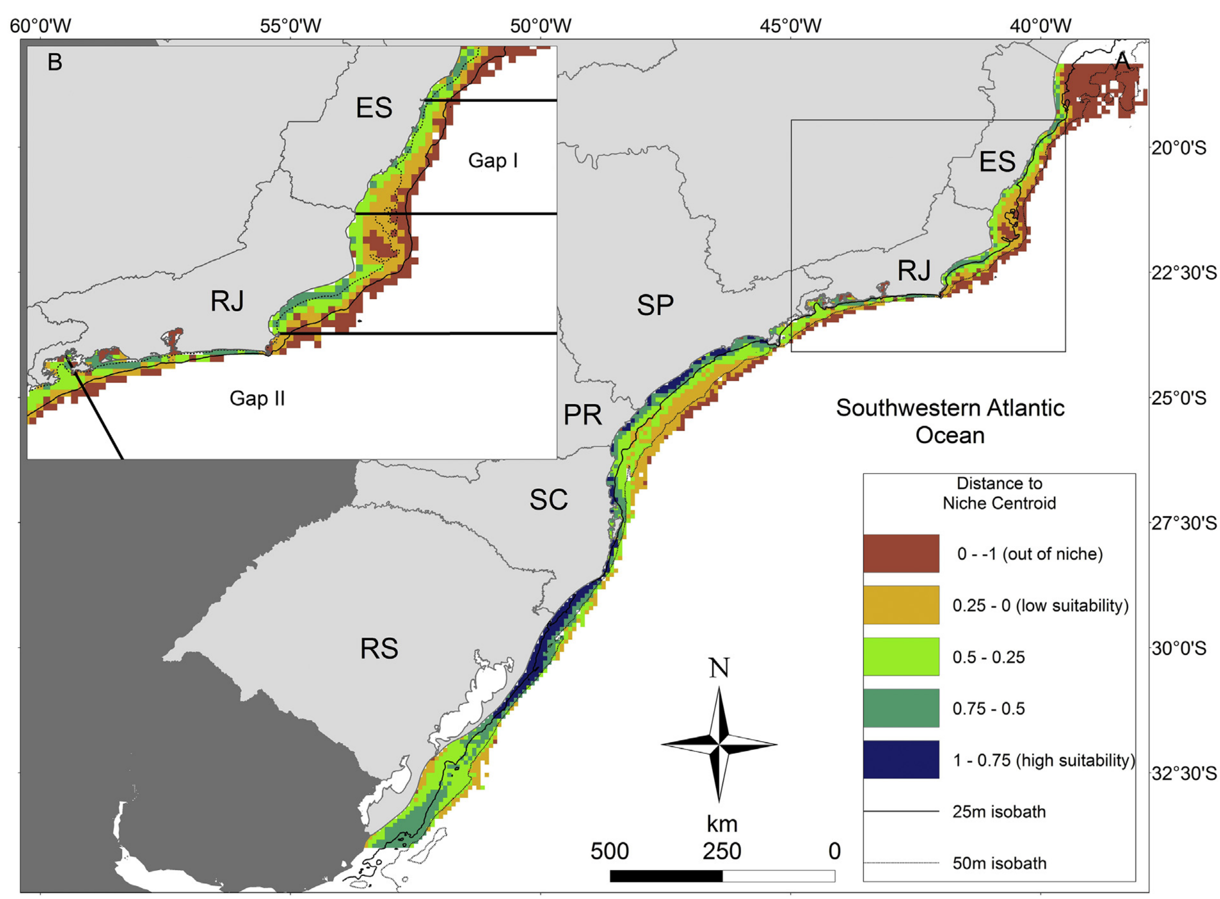

Fig. 7. A) Habitat suitability model with continuous values of the distance to the niche centroid representing the franciscana's fundamental niche. B) A map zoom is provided to visualize the environmental suitability of northern and southern distributional gaps. Values between 0 and 1 represent the relative distance between the points and the centre of the ellipsoid; −1 represent areas out of the ellipsoid or unsuitable; 0 means areas on the edge of the ellipsoid or with low suitability; and 1 means areas on the center of the ellipsoid or with high environmental suitability (H. Qiao 2017, p.c.).

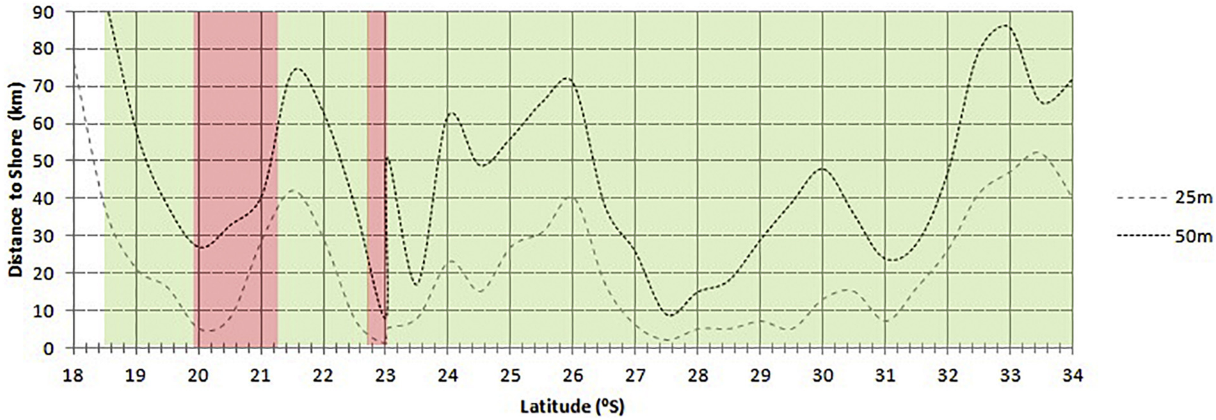

Fig. 8. Distance to shore of the 25 m and 50 m isobaths in relation to latitude. Area occupied by franciscana are represented in green; distributional gaps are represented in red (left, Gap I; right, Gap II). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

play a key role to explain for the absence of franciscana in these areas.

5. Conclusions

The shelf habitat is very important to franciscana. However, a wide shelf does not necessarily result in an increased presence of franciscana if other conditions such as salinity are not suitable. For example, the Brazilian continental shelf is very large at the north portion of the Espírito Santo, in the region of the Abrolhos Bank, however franciscana range seems to be limited longitudinally, possible due to higher and salt levels recorded there.

The new limits of FMAs and the habitat suitability model presented here could be used as a guide to planning studies and actions that aim the conservation of the franciscana in Brazil. Further studies should investigate franciscanas' prey availability in those areas considered distributional gaps as well the possible relevance of other biotic interactions. Finally, changes in the coastal environment and habitat loss caused by human activities, such as industrial port development, should also be considered in conservation plans for the species.

Acknowledgements

We would especially like thank Dr. Maria João Ramos Pereira, Dr. Manoel Fontoura, Dr. Vanderlei Debastani, Dr. Luis E. Escobar, and Dr. Robert S. Schick for commenting of early drafts of this paper. We thank Dr. A. Townsend Peterson, Dr. Huiji Qiao, and Dr. Luis E. Escobar for their support in methodology. This research is part of KBA PhD study at the Universidade Federal do Rio Grande do Sul at Programa de Pós-Graduação em Biologia Animal, who received a PhD Degree scholarship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) (Grant 1395438).This work was partly supported by grants from the US Marine Mammal Commission (Grant E4026227), and the International Whaling Commission Voluntary Fund for Small Cetaceans to Instituto Aqualie and from Fundo Nacional do Meio Ambiente (FNMA), Cetacean Society International, International Union for Conservation of Nature and Fundação O Boticário de Proteção à Natureza to GEMARS. Programa Petrobras Ambiental sponsored the Projeto Toninhas/UNIVILLE in the period of 2011 to 2015. CNPq also provided a Research Fellowship to EcoMega-FURG (PQ 307843/2014-0). Funding for fieldwork was partly granted by Yaqu Pacha (Germany) to EcoMega-FURG. The research groups "Ecologia e Conservação da Megafauna Marinha-EcoMega/CNPq", and "Ecologia e Conservação de Organismos e Ambientes Aquáticos-ECOAqua/CNPq" participated in this study. This is a contribution of the "Evolução e Biodiversidade de Cetáceos/CNPq" research group and "Distribution and abundance of franciscana dolphin in Brazil" Project (www.researchgate.net).

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