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Ecological niche modeling of *Stenella* dolphins (Cetartiodactyla: Delphinidae) in the southwestern Atlantic Ocean

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ABSTRACT

Since the Moreno's et al. (2005) work, no study was done to update the distribution patterns of *Stenella* dolphins in the southwestern Atlantic Ocean. Ecological niche modeling was used to redefine the distribution patterns of *Stenella* dolphins in this area of Atlantic Ocean. Maximum entropy method (Maxent) was employed to generate models using a set of environmental variables as explanatory variables of the location records obtained by sighting and accidental captures. All ecological niche models performed returned AUC values >0.9. Areas with high environmental suitability for pantropical spotted dolphin (*Stenella attenuata*), Clymene dolphin (*Stenella clymene*) and spinner dolphins (*Stenella longirostris*) are found in warm (>25 °C) and deep waters (≥1000 m). High environmental suitability for Atlantic spotted dolphin (*Stenella frontalis*) seems to occur between 20.5°S and 30°S in the southeastern Brazilian coastal waters. The projected maps of species distributions showed patterns closely related to environmental changes at a fine spatial scale and added valuable information about the offshore limits of those oceanic species. The results suggest that the different species of *Stenella* have distinct environmental requirements in the southwestern Atlantic Ocean.

1. Introduction

Most of the knowledge about species distribution is represented in coarse-scale maps, as part of field guides or in public databases (*e.g.* the Red List of The International Union for Conservation of Nature), which in most cases represent a generalization based on the accumulated knowledge about the distribution of species over time (see Gaston and Fuller, 2009). This representation is perhaps more challenging in marine organisms, due to the difficulty of obtaining data on species locations and also to the limited sampling effort in many offshore areas (Kaschner et al., 2006; Tyberghein et al., 2012). Moreover, there is a significant lack of knowledge on the ecology and habitat preferences of a great number of cetaceans (Ready et al., 2010; Redfern et al., 2006). Currently, the description of cetacean range is mainly based on oceanographic features (Palacios et al., 2013) and little is known about the offshore limits of the species. Furthermore, the marine environment appears to be homogeneous enough to support the distribution of species over a broad geographic range, but local variations in habitat features may also contribute to the development of local niche specializations (Hoelzel, 1998). Surface water masses show considerable variation in depth, salinity, temperature, pressure, light attenuation, nutrient levels, dissolved oxygen, and biological production, crucial factors that play important roles in determining species distributions and supporting processes of ecological and genetic subdivision of populations (Norris, 2000).

The genus *Stenella* Gray, 1866 is one of the most representatives of the family Delphinidae, although widely recognized as non-monophyletic (Amaral et al., 2012b; Kingston et al., 2009; Leduc et al., 1999; Moreno et al., 2005; Perrin et al., 2013). The five species included in the genus *Stenella* are distributed in tropical, subtropical and temperate waters, of which the pantropical spotted dolphin (*Stenella attenuata*, hereafter pantropical spotted dolphin) (Gray, 1846), the spinner dolphin (*Stenella longirostris*, hereafter spinner dolphin) (Gray, 1828) and the striped dolphin (*Stenella coeruleoalba*, hereafter striped dolphin) (Meyen, 1833) inhabit the Atlantic, Pacific and Indian Oceans, while the Atlantic spotted dolphin (*Stenella frontalis*, hereafter Atlantic spotted dolphin) (Cuvier, 1829) and the Clymene dolphin (*Stenella clymene*, hereafter Clymene

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dolphin) (Gray, 1850) are endemic to the Atlantic (Fertl et al., 2003; Jefferson et al., 2008; Moreno et al., 2005; Perrin et al., 2009).

In the Atlantic Ocean, most of the studies concerning cetacean distribution and habitat preferences have concentrated in the North Atlantic (*e.g.* Baumgartner et al., 2001; Cañadas et al., 2002; Davis et al., 1998; Davis et al., 2002; Jefferson, 1996). Conversely, in the southwestern Atlantic Ocean (hereafter, SWA) most of the studies were based solely on a few localized records of occurrence from strandings, accidental captures or sightings (Lucena et al., 1998; Ott and Danilewicz, 1996; Pinedo and Castelo, 1980; Secchi and Siciliano, 1995; Siciliano, 1994; Simões-Lopes and Ximénez, 1993; Ximénez and Praderi, 1992; Zerbini and Kotas, 1998). The only comprehensive study of the geographic distribution of the genus *Stenella* in the SWA was conducted by Moreno et al. (2005), who reviewed capture, sightings and stranding records to describe distribution and habitat preferences of each species in this region with respect to oceanographic features (*i.e.* major water masses) and ocean topography (*i.e.* depth).

Ecological niche modeling (*sensu* Warren, 2012) is a widely used tool (Elith et al., 2010) that in this study was employed to investigate species distributional limits. The main focus of ecological niche modeling is to relate known locations of a species with the environmental characteristics of these locations, and predict the potential geographical range of that species based on those relations (Austin et al., 2006; Elith and Leathwick, 2009).

A wide range of methods has been used to predict the species distribution and for some species detailed presence and absence occurrence data are available, allowing the use of a variety of techniques (Phillips et al., 2006). However, absence data are not available for most species, particularly for marine mammals, and presence-only methods are being used successfully to predict cetacean distribution (Édren et al., 2010; Friedlaender et al., 2011; Moura et al., 2012; Thorne et al., 2012).

One of these presence-only modeling approaches is the Maximum Entropy method — Maxent (Phillips and Dudík, 2008; Phillips et al., 2006,). The Maxent software is one the most popular tools for species distribution and environmental niche modeling (Merow et al., 2013) and has been used successfully for limited and/or sparse datasets and species (Elith et al., 2011; Wisz et al., 2008). Furthermore comparative similarity measures and statistical tests were developed by Warren et al. (2008) and implemented in software ENMTools (Warren et al., 2010) which interacts with Maxent.

Adding data to that previously compiled by Moreno et al. (2005), this study aimed to refine the distribution patterns of *Stenella* dolphins in the SWA in order to increasing ecological insight about the species of this genus using Maxent.

2. Methods

2.1. Study area

Considering the large cetaceans dispersal ability and not obvious geographical barriers to dolphins, the geographical extent of the models and the background sampling was restrict to the SWA, which comprises waters south of Equator and west of 20°W (Moreno et al., 2005; Tavares et al., 2010). This area is under the domain of the high pressure center of the Atlantic anticyclone which controls the climate and determines the large-scale oceanographic circulation. The main currents of the SWA are the South Equatorial, Brazil and Malvinas Currents (Moreno et al., 2005; Seeliger et al., 1997; Tavares et al., 2010).

2.2. Occurrence data

Georeferenced occurrence data for each *Stenella* species in the SWA were compiled from literature (Appendix 1). Unpublished data recorded after 2005 were also included. Most sighting data were collected during opportunistic and dedicated ship surveys in different seasons. Opportunistic sightings were recorded by both experienced and non-experienced marine mammal observers on board fishing or research vessels. Several information were collected and photographs were taken when a group of dolphins was sighted (*e.g.* date, geographical coordinates, species identification to the lowest possible taxon, estimated number of individuals, presence of calves and behavioral observations). Systematic ship surveys included several cruises conducted along Brazilian coast (Table 1).

A total of 140 sightings/captures were used in this study (Fig. 1, Table 2, Appendix 1). Only records that could be unequivocally identified to species level through photographic record or experienced recorder who identified the species at the time of sighting/capture were included (*sensu* Moreno et al., 2005).

2.3. Environmental data

Environmental layers were selected based on previous cetacean habitat studies (Baumgartner et al., 2001; Cañadas et al., 2002; Davis et al., 2002). Bathymetry was included as a topographic layer. Hydrographical layers such as concentration of chlorophyll A (hereafter, chlor. A), diffuse attenuation (hereafter, D.A.), salinity and sea surface temperature (hereafter, SST) were included in three relevant metrics: annual maximum, minimum and mean. For SST and chlor. A, the annual range (difference between maximum and minimum) was used as well. The layers were gathered from Bio-Oracle (Oceans Rasters for Analysis of Climate and Environment) (Tyberghein et al., 2012) and ETOPO1 Global Relief Model (Amante and Eakins, 2009). All the 13 environmental layers were processed in ArcGIS 10.2.2 in datum WGS 84, with the same spatial extent (5°N–10°W to 55°S–70°W) and the same resolution (9.2 km).

2.4. Ecological niche modeling

Maxent 3.3.3 k software (Phillips et al., 2006) was used to model the potential distribution of all species of genus *Stenella* in the SWA. Maxent randomly selected 70% of the occurrence localities as training data, whereas the remaining 30% were reserved for testing the resulting models. The default Maxent settings was used, which according Merow

Table 1
Systematic and opportunistic (*) surveys conducted in the SWA from which records from *Stenella* were analyzed. The data of each *Stenella* sighting is available on Appendix 1.

Project/cruise	Year	Surveyed area	Source information
Revizee — Score Sul project	1996–1997	Southeastern/Southern Brazilian Coast	Zerbini et al., 2004a; Tavares et al., 2010
Minke Whale project	1998–2001	Northeastern Brazilian Coast	Zerbini et al., 2000; Zerbini et al., 2004b; Tavares et al., 2010
Yavox Mobile*	2001	Southeastern Brazilian Coast	Moreno et al., 2005
Campos Basin	2004–2005	Southeastern Brazilian Coast	Tavares et al., 2010
Habitats project	2005	Southeastern Brazilian Coast	This study
Piatam Norte	2008	North Brazilian Coast	This study
Talude project	2010	Southeastern / Southern Brazilian Coast	Secchi and Di Tullio per. comm.
Pro-Trindade I	2012	Northeastern /Southeastern Brazilian Coast and Vitória–Trindade Chain	This study

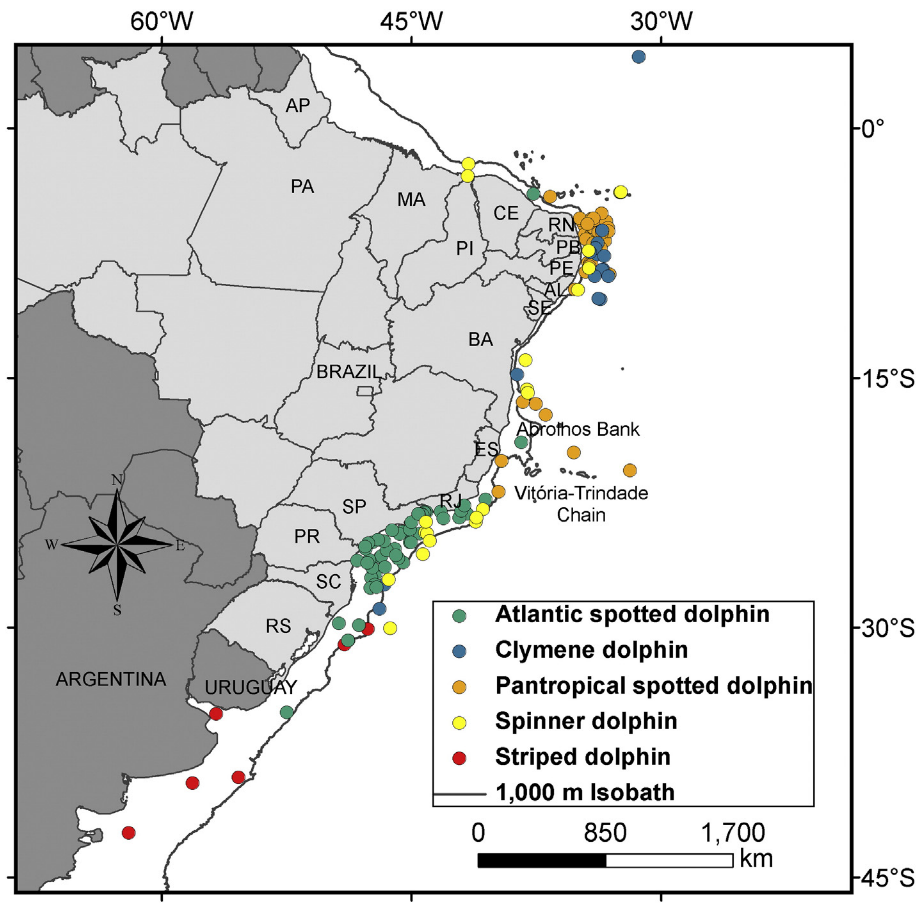

Fig. 1. Map showing records of Atlantic spotted dolphins (*Stenella frontalis*), Clymene dolphin (*S. clymene*), pantropical spotted dolphin (*S. attenuata*), spinner dolphin (*S. longirostris*) and striped dolphin (*S. coeruleoalba*) in the southwestern Atlantic Ocean (SWA).

et al. (2013) assumes that the species is equally likely to be in anywhere on the landscape. In this way Maxent predicts a distribution that is as spatially diffuse as possible, which tends to predict the largest possible range size consistent with the data.

The receiver operating characteristic (ROC) analysis and the area under the curve (AUC) were used to provide a single measure of model performance, independent of any particular choice of threshold (Phillips et al., 2006). A random prediction results in an AUC equal to 0.5 and with presence-only data, the maximum achievable AUC is less than 1 (Phillips et al., 2006).

To investigate the degree of overlap between the *Stenella* species distributions, the equal test sensitivity and specificity threshold from Maxent was selected to generate pairwise maps using the Intersect tool available in ArcGIS 10.2.2.

2.5. Statistical comparisons of distribution patterns

In order to test the null hypothesis assuming that each species had similar distributions taking consideration to environmental variables (bathymetry, salinity, annual mean of concentration of chlor. A, annual mean of D.A., annual mean and annual range of SST) was used the Kruskal–Wallis test in SYSTAT 13.

To compare the predicted habitat suitability of ecological niche model generated for each species of *Stenella* comparative similarity measures and the niche identity test introduced by Warren et al. (2008) and implemented in the ENMTools 1.3 software were used. ENMTools measures niche overlap using two similarity measures: Schoener's D and I statistic, which is derived from Hellingers' distance. Both similarity measures range from 0 (when species predicted

Table 2
AUC values, number of records used as training and test data and relative contributions of the major environmental variables to the Maxent models.

Species	Training AUC	Training data	Test AUC	Test data	Variable contribution
Pantropical spotted dolphin	0.992	n = 32	0.990	n = 13	Min. SST (29.4%) Max. Chlor. A (15.7%)
Clymene dolphin	0.943	n = 12	0.978	n = 4	Min. SST (52.3%) Max. D.A. (10.3%)
Striped dolphin	0.957	n = 5	0.969	n = 1	Bathymetry (81.4%) Range SST (14.8%)
Atlantic spotted dolphin	0.995	n = 37	0.994	n = 15	Bathymetry (53.6%) Min. SST (26.2%)
Spinner dolphin	0.988	n = 15	0.984	n = 6	Bathymetry (55.6%) Max. Chlor. A (12.9%)

environmental tolerances do not overlap at all) to 1 (when all grid cells are estimated to be equally suitable for both species) (Warren et al., 2010). The niche identity test, which tests whether the ecological niche models by two species are identical, were conducted with 1000 iterations for each comparison.

3. Results

3.1. Ecological niche modeling

Ecological niche models generated for all *Stenella* species returned AUC values higher than 0.9 (Table 2). The potential geographical range of the species is shown in Figs. 2, 3, 4, 5 and 6.

3.1.1. Ecological niche model for pantropical spotted dolphin (S. attenuata)

This model (Fig. 2) indicates that highly suitable areas for the occurrence of pantropical spotted dolphin (>70%) are in waters with high SST (>27 °C), low temperature range (around 2.5 °C) and deeper than 1000 m located in the northeastern Brazilian coast. Environmental suitability levels between 40–70% are found surrounding the Vitória–Trindade Chain (about 20.5°S); suitability drops to less than 20% south of this region.

3.1.2. Ecological niche model for Clymene dolphin (S. clymene)

The model (Fig. 3) shows a wide area of high environmental suitability (60–80%) in the SWA. Warm waters of low latitudes (0° and 15°S) characterized by low temperature range, depths above 1000 m and close to the continental shelf break present levels of suitability between 70% and 90%. South of the Vitória–Trindade Chain environmental suitability falls below 60% and decreases southward. Environmental suitability near the southernmost record (28.86°S, 46.93°W; record 48 in Appendix 1) was equals to 21%.

3.1.3. Ecological niche model for striped dolphin (S. coeruleoalba)

Because only six records were available in the SWA for this species, the resulting model (Fig. 4) should be taking with caution. Environmental suitability levels above 70% are found south of 25°S, increasing to around 80% in the Argentinean coast. Levels of suitability between 50–60% seem to occur along the continental shelf break in the northern, northeastern and southeastern Brazilian coast.

3.1.4. Ecological niche model for Atlantic spotted dolphin (S. frontalis)

This model (Fig. 5) showed that areas with environmental suitability above 60–70% are found between 23°S and 27°S in coastal waters (<200 m) around 23 °C of SST and high temperature range (ca. 5 °C). The northern Brazilian coast shows above 10% of environmental suitability. In the Abrolhos Bank, the unique record in this region (18.86°S, 38.41°W; record 118 in Appendix 1) reaches 9% of environmental suitability and the values of bathymetry, annual mean and annual range of SST are 47 m, 26 °C and 3.58 °C, respectively. The southernmost record obtained in Uruguayan waters (35.08°S, 52.49°W; record 119 in Appendix 1) reaches only 5% of environmental suitability, where the respective values of bathymetry, annual mean and annual range of SST are 134 m, 18 °C and 10 °C.

3.1.5. Ecological niche model for spinner dolphin (S. longirostris)

The model generated (Fig. 6) indicates environmental suitability above 70% from 1°S to approximately 28.5°S in waters up to 1000 m and along the continental shelf break where temperature ranges from 24 °C to 28 °C. Waters surrounding islands and along the Vitória–Trindade Chain show high environmental suitability (70–80%). The southernmost

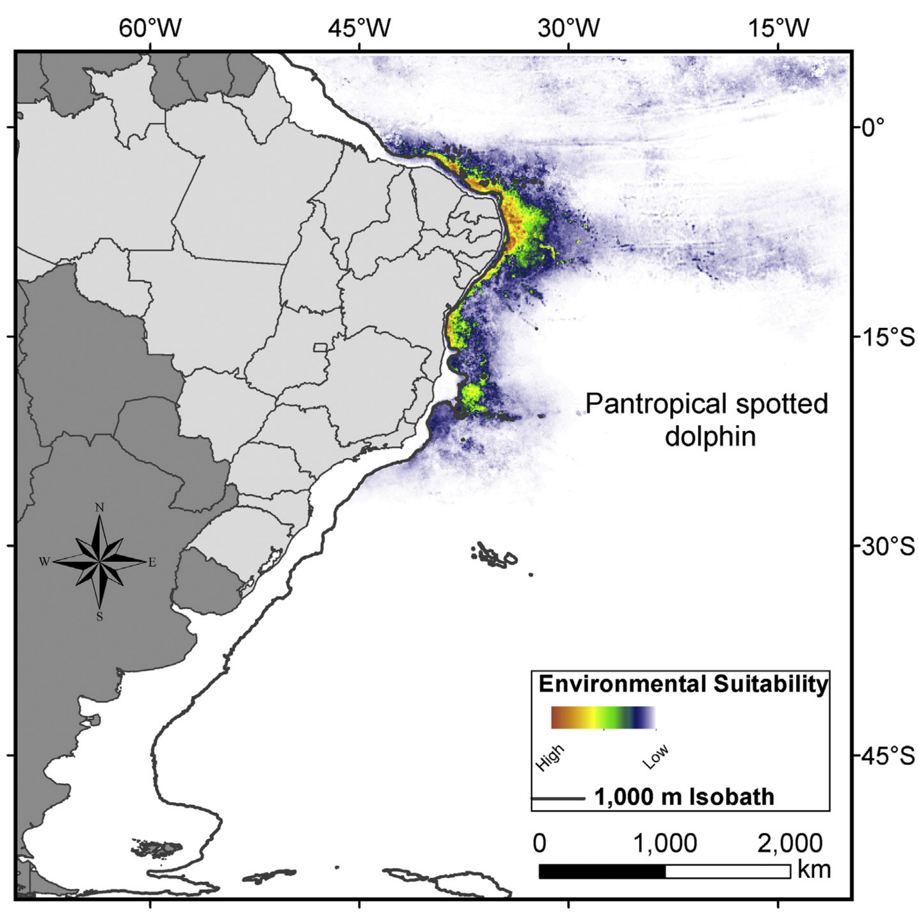

Fig. 2. Potential geographic distribution for pantropical spotted dolphin (*S. attenuata*) in the SWA.

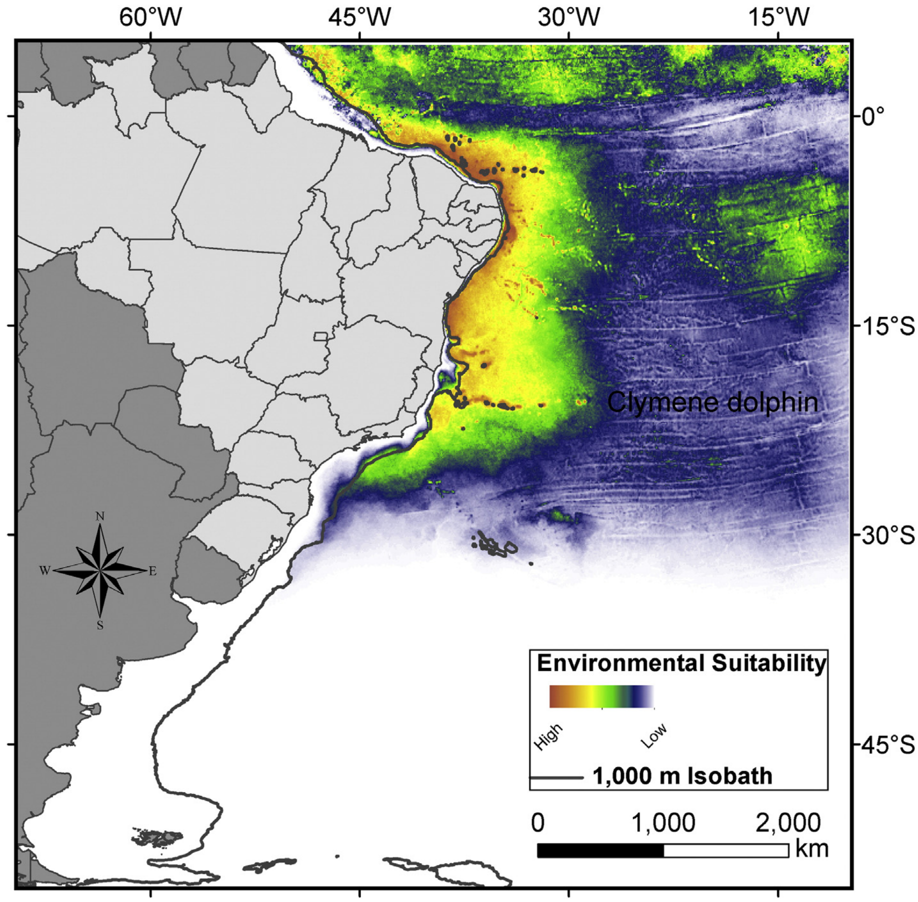

Fig. 3. Potential geographic distribution for Clymene dolphin (*S. clymene*) in the SWA.

record (30.4°S, 46.29°W; record 123 in Appendix 1) returned less than 20% of environmental suitability.

3.2. Niche overlap and identity test

Similarity measures of pairwise *Stenella* species are presented below (Table 3). For all pairwise comparisons in the identity test, the similarity score for ecological niche models built from the occurrences of the two species under comparison is lower than expected based on the null hypothesis of niche equivalence (C.I. 99.9%), therefore all null hypothesis of equivalent environmental niches among species were rejected.

The overlap map based in the presence/absence predictions indicates an extensive spatial overlap of pantropical spotted and Clymene dolphins (Fig. 7A). These two species may exhibit habitat partitioning, although this partitioning does not imply a total spatial separation in the northeastern Brazilian coast.

On the other hand there seems to exist an almost complete spatial separation and, possibly, habitat partitioning of pantropical and Atlantic spotted dolphins in the SWA (Fig. 8A), as happens with Clymene and Atlantic spotted dolphins (Fig. 9A).

Pantropical spotted and spinner dolphins show a contact zone along the Brazilian coast on waters approximately 1000 m deep and above the Vitória–Trindade Chain (Fig. 10A). However, pantropical spotted dolphin occurs in oceanic waters, whereas spinner dolphin occurs mostly in the outer continental shelf.

The overlap map of Clymene and spinner dolphins shows a narrow contact zone along the Brazilian coast, mainly on waters approximately 1000 m deep in the northeastern portion of the Brazilian coast and alongside the Vitória–Trindade Chain (Fig. 11A).

Finally, there seems to be a partial spatial overlap of the ranges of Atlantic spotted and spinner dolphins (Fig. 12A). However, these two species may exhibit habitat partitioning, but this partitioning does not imply total spatial separation.

3.3. Statistical comparisons of environmental variables

The median of environmental variables for each species indicated significant interspecies differences (Fig. 13). The null hypothesis of equal medians for bathymetry, salinity, annual mean of concentration of chlor. A, annual mean of D.A., annual mean and annual range of SST was rejected (Kruskal–Wallis test, $p \leq 0.001$). However, pantropical spotted and Clymene dolphins showed more similar medians when compared with the other species of *Stenella*. These species occur in areas of low productivity, deeper and warmer waters with approximately 2.5 °C of temperature range. Spinner dolphin occupies areas up to about 1000 m deep with low productivity, and with temperature ranges up to 5 °C. Atlantic spotted dolphin inhabits shallow waters, with lower temperature and temperature ranges greater than 5 °C but with higher productivity.

4. Discussion

Recent studies show consistent intraspecific differences in morphology, ecology, genetics and habitat choice by delphinids in several regions (*e.g.* western North Atlantic: Adams and Rosel (2006); New Zealand: Tezanos-Pinto et al. (2009); southern Australia: Charlton-Robb et al. (2011); large geographic scale: Amaral et al. (2012a); Andrews et al. (2013); Morin et al. (2010); Natoli et al. (2004); Natoli et al. (2006)). However, explaining the structuring of assemblages in apparently homogeneous environments such as the open ocean is a major ecological and evolutionary question (Norris, 2000). In fact, the requirement of isolation during allopatric speciation appears to be

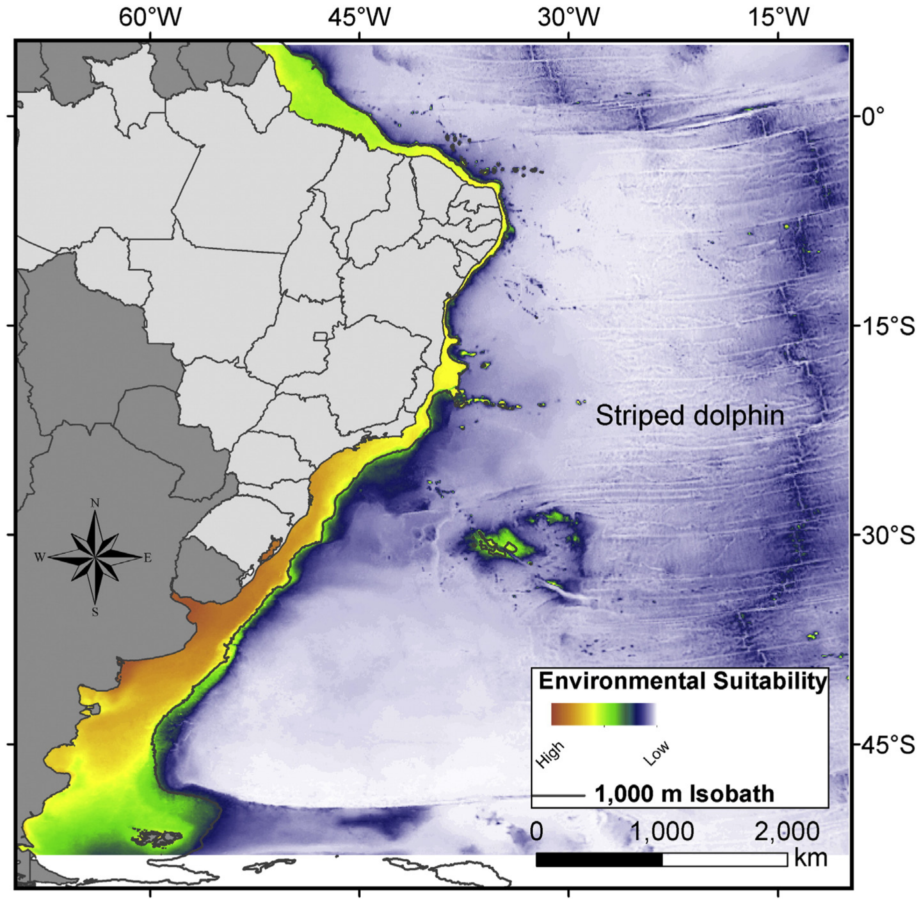

Fig. 4. Potential geographic distribution for striped dolphin (*S. coeruleoalba*) in the SWA.

harder to satisfy in the ocean — the so called marine-speciation paradox (Bierne et al., 2003). Alternatively to this point of view, the population structure in the marine realm is overturning the notion of large and homogeneous marine population limiting local adaptation and speciation as observed to fishes (Hauser and Carvalho, 2008) and recently to dolphins (Viricel and Rosel, 2014).

This paper discuss the species-habitat relationships in the marine environmental using the ecological niche modeling tool, which has been conducted almost entirely in terrestrial systems. The ecological niches of cetaceans seem to be defined by water temperature, water depth and factors that affect the distribution and abundance of their prey (topography, ocean currents and primary productivity) (Baumgartner et al., 2001; MacLeod, 2009; Palacios et al., 2013). Although, the main influence on geographic ranges of cetaceans species appears to be water temperature (MacLeod, 2009). The results presented here indicate that the SWA offers differentiated niches for each *Stenella* species. For example, tropical waters (salinity of 36, SST >20 °C) (Emílsson, 1961) off the northeastern Brazilian coast have the highest environmental suitability (>60%) for pantropical spotted, Clymene and spinner dolphins. These species also find a suitable area in the Abrolhos Bank, a major Brazilian marine ecosystem. The Vitória–Trindade Chain seems to act as a southern barrier for the distribution of *Stenella* species, given the observed substantial decrease of environmental suitability south of this chain.

The ecological niche model for pantropical spotted dolphin indicates that the suitable environmental conditions for this species start to significantly decrease around 20°S, which is similar to the 23°S southern limit proposed by Moreno et al. (2005) based on strandings and sightings. However, the model suggests a more restricted distribution showing a smaller longitudinally area of occurrence contrary to the proposed by Moreno et al. (2005).

The model generated for Clymene dolphin is the only model that shows a wide distribution pattern agreeing with records in pelagic waters between American and African continents (Fertl et al., 2003; Perrin et al., 1981). The model indicates 60–80% environmental suitability in waters among 2000–4000 m deep and beyond continental shelf. Indeed, although the Clymene dolphin seems to be essentially tropical, records in the states of Santa Catarina (SC) (Simões-Lopes et al., 1994) and Rio Grande do Sul (RS) (Fertl et al., 2003) denote that the species occur south of tropical waters, despite the low environmental suitability of this region reflected by the model (around 20%).

Spinner dolphin seems to have similar habits to those of pantropical spotted dolphin. However, the former tolerates a broader temperature range and seems to displace with the Brazil Current as far south as 30°S, where this current meets the cooler Malvinas Current (Secchi and Siciliano, 1995).

Only six records were used for modeling striped dolphin in the SWA, because it was decided to use highly reliable observations. Two unconfirmed records in Brazilian coast were not included (Maia-Nogueira et al., 2001; Pinedo and Castello, 1980). The limited data result from observations and incidental captures recorded mainly in cold and shallow waters off Argentina and southern Brazil (Bastida et al., 2001; Moreno et al., 2005; E. Secchi and J. Di Tullio, pers. comm.). The resulting model, as expected with such limited amount of records, simply indicates that the species occurs in waters with those features. Strandings are also more frequent in the southernmost areas of the SWA (Uruguay and Argentina: Bastida et al., 2001; Brownell and Praderi, 1976; Castro et al., 2011; Ximénez et al., 1972; Ximénez and Praderi, 1992; southern Brazil: Ott and Danilewicz, 1996; Pinedo and Castello, 1980). Although strandings were reported in the northeastern and southeastern Brazilian coast (Lucena et al., 1998; Maia-Nogueira et al., 2001; Rosas et al., 2002). Moreno et al. (2005) had already stated

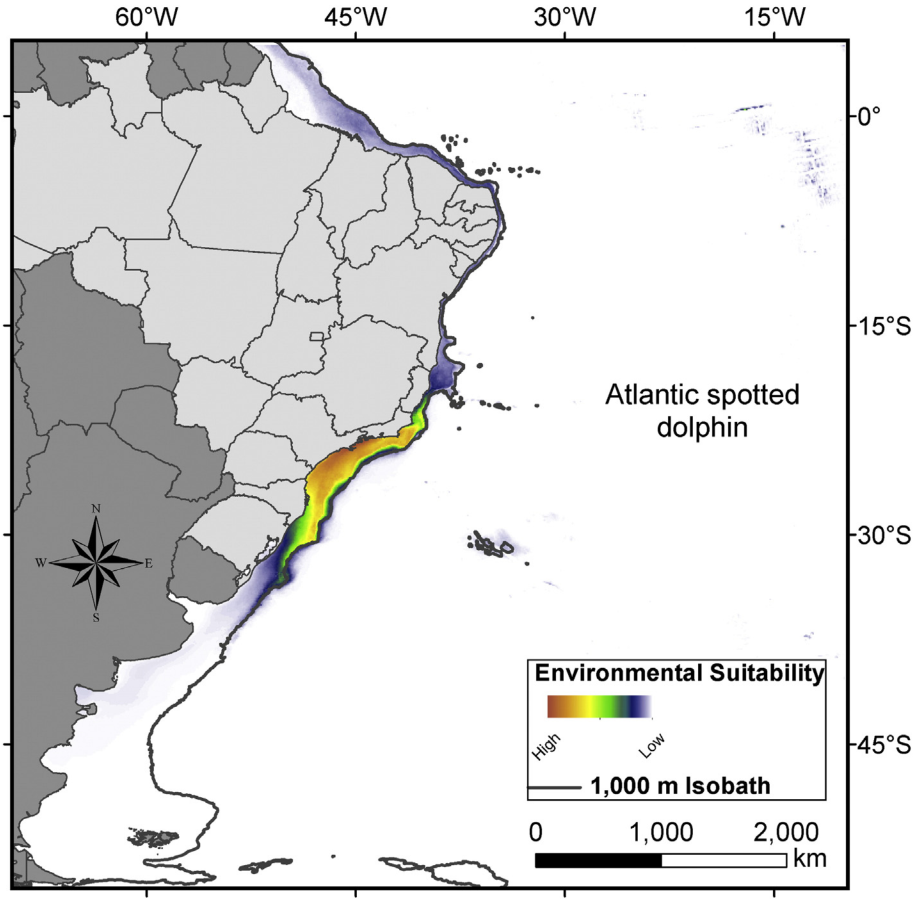

Fig. 5. Potential geographic distributions for Atlantic spotted dolphin (*S. frontalis*) in the SWA.

that this was the least known species of *Stenella* in the SWA; since their study, few records were recorded and added to the database, which strongly suggests that striped dolphin is rare in this region.

Atlantic spotted dolphin is the only species that shows strictly coastal habits in the SWA, occurring over the continental shelf and slope up to 1000 m depth. Sightings and strandings at about 30°S concur with the area of the Subtropical Convergence Zone (Seeliger et al., 1997). This pattern suggests that the distribution range of the species is seasonally influenced by the drift of the Brazil Current trough southern Brazil (Moreno et al., 2005) and Uruguay (Paro et al., 2014). Moreno et al. (2005) observed an absence of Atlantic spotted dolphin between 6°S and 21°S and suggested that this species has a discontinuous distribution along the Brazilian coast. These authors proposed the existence of two subpopulations in South America, one occurring off the southeastern Brazilian coast (between 21°S and 33°S) and another distributed north of 6°S. Recently, new records extended the distribution of the southeastern population further north in waters adjacent to the Abrolhos Bank at 18°S (Danilewicz et al., 2013) and further south in Uruguayan waters (Paro et al., 2014). The model indicates that the environmental suitability for this species decreases to 10–15% in the Abrolhos Bank while north of 16°S the suitability is around 5–10% showing that the rare occurrences of Atlantic spotted dolphin in this region are probably related with the lack of environmental conditions for the species. Although there is a lack of dedicated research efforts in the northern coast of Brazil (between the states of Amapá (AP) and Maranhão (MA)) it is possible suggest that the environmental conditions of the south/southeastern population is different from those of the north/northeastern population, as revealed by morphological (Moreno, 2002; Moreno et al., 2005) and molecular data (Caballero et al., 2013). Indeed, ecological niche modeling is a power tool able to provide evidence for populations or species distinction given that intraspecific specialization reflect differences in habitat use and this can be detected by modeling (Hawlitschek et al., 2011; Warren et al., 2010). In this sense, the isolated southwestern Atlantic population of Atlantic spotted dolphin distributed from 18°S to 35°S in the SWA should be managed as a different conservation unit due to the threats of anthropogenic origin this population is facing (namely coastal degradation, oil exploration, and pollution) (Japenga et al., 1988; Kjerfve et al., 1997; Leonel et al., 2012).

The high performance of the ecological niche models, reflected by the AUC values probably relate to the quality of the predictors used in the training phase. Bio-Oracle environmental layers, used here as predictors, reach extremely high AUC values for both training and test data, because this dataset is able to capture the macroecological preferences of the species and, when correctly used, allow the building of highly accurate species distribution models for marine species (Tyberghein et al., 2012).

When compared with the distribution maps available in the literature (*e.g.* Fertl et al., 2003; Folkens et al., 2002; Jefferson et al., 2008; Moreno et al., 2005; Perrin et al., 2009), the predicted potential geographic distributions presented here show more restricted areas suitable to the presence of *Stenella* species. Absence of significant environmental predictors and few or concentrated samples in inshore areas used to model training could reflect shortcomings. However, ecological niche models present in this study indicate areas of very high environmental suitability for each *Stenella* species in the SWA that also agree with the *Stenella* stranding pattern for each species (Moreno et al., 2005). Furthermore, the restricted pattern distribution obtained for the genus is consistent with the results of recent studies. In this way it is possible to agree with many of these studies when they suggest that most species are certainly not cosmopolitan and

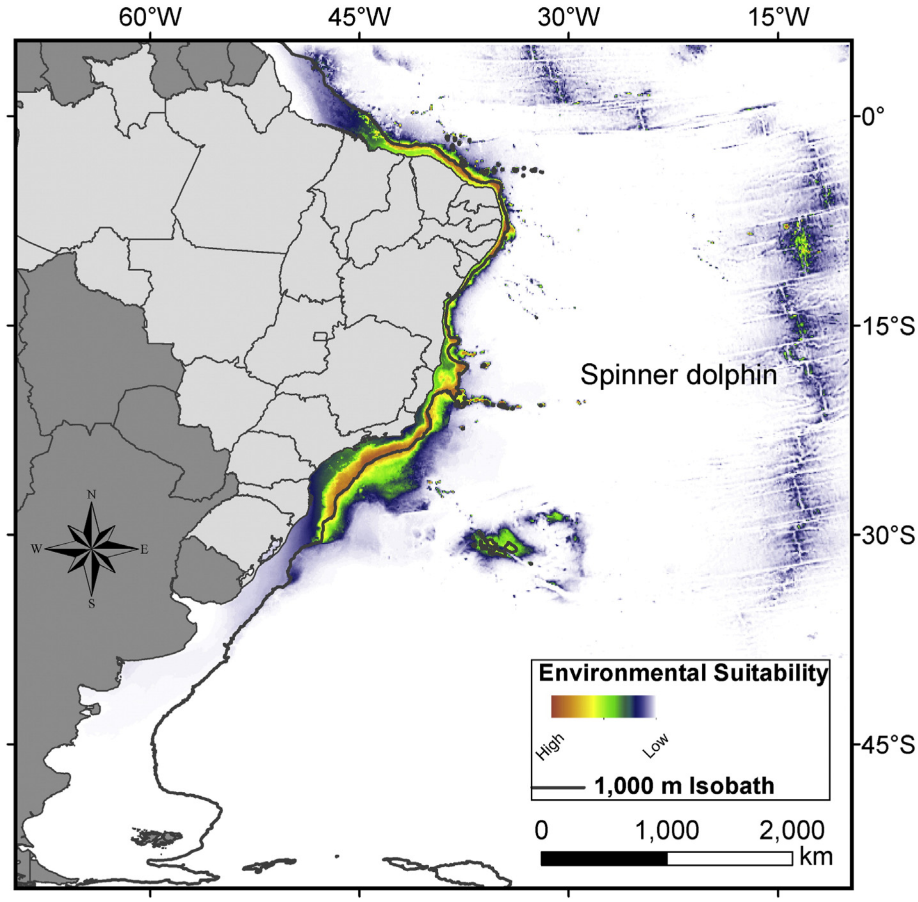

Fig. 6. Potential geographic distribution for spinner dolphin (*S. longirostris*) in the SWA.

those species traditionally seen as widely distributed might, instead, be a set of subspecies or even different species (Chivers et al., 2005; Hoelzel, 1998; Morin et al., 2010; Tezanos-Pinto et al., 2009; Viricel and Rosel, 2014). Among the Delphinidae, killer whale (*Orcinus orca*) and bottlenose dolphin (*Tursiops truncatus*) are examples of this new perspective that elevate different ecotypes to full species demonstrating that if fact some cetacean species are adapted to a local niches (see Charlton-Robb et al., 2011; Morin et al., 2010; Tezanos-Pinto et al., 2009).

Understand the niche segregation at the multi-species community level is critical in ecology, especially to investigate the role of organisms within a community. Furthermore, this question may be challenging for a large marine top predators (Kiszka et al., 2012). Bearzi (2005a) presents a review of some well-studied dolphin species found in simpatry, which sympatric dolphins seem to use different strategies to co-exist. Studies such as conducted by Baumgartner et al. (2001) in Gulf of Mexico and by Bearzi (2005b) in Santa Monica Bay, California argue the existence of habitat partitioning among sympatric species. Here, it is proposed an alternative method to access ecological aspects of sympatric species by adding information from ecological niche modeling and overlap maps. The results obtained suggest that *Stenella* species exhibit habitat partitioning due to the differences in their environmental

Table 3
Metrics obtained in overlap and identity tests conducted between pairwise *Stenella* species.

Pairwise *Stenella* species	Niche overlap test	Identity test
Pantropical spotted dolphin and Clymene dolphin	D = 0.453	D = 0.689 ± 0.080
	I = 0.763	I = 0.902 ± 0.053
Pantropical spotted dolphin and Atlantic spotted dolphin	D = 0.033	D = 0.814 ± 0.033
	I = 0.090	I = 0.964 ± 0.011
Pantropical spotted dolphin and Spinner dolphin	D = 0.240	D = 0.735 ± 0.061
	I = 0.462	I = 0.926 ± 0.033
Clymene dolphin and Atlantic spotted dolphin	D = 0.051	D = 0.654 ± 0.062
	I = 0.151	I = 0.884 ± 0.042
Clymene dolphin and Spinner dolphin	D = 0.278	D = 0.716 ± 0.071
	I = 0.550	I = 0.918 ± 0.039
Atlantic spotted dolphin and Spinner dolphin	D = 0.335	D = 0.778 ± 0.061
	I = 0.646	I = 0.945 ± 0.027

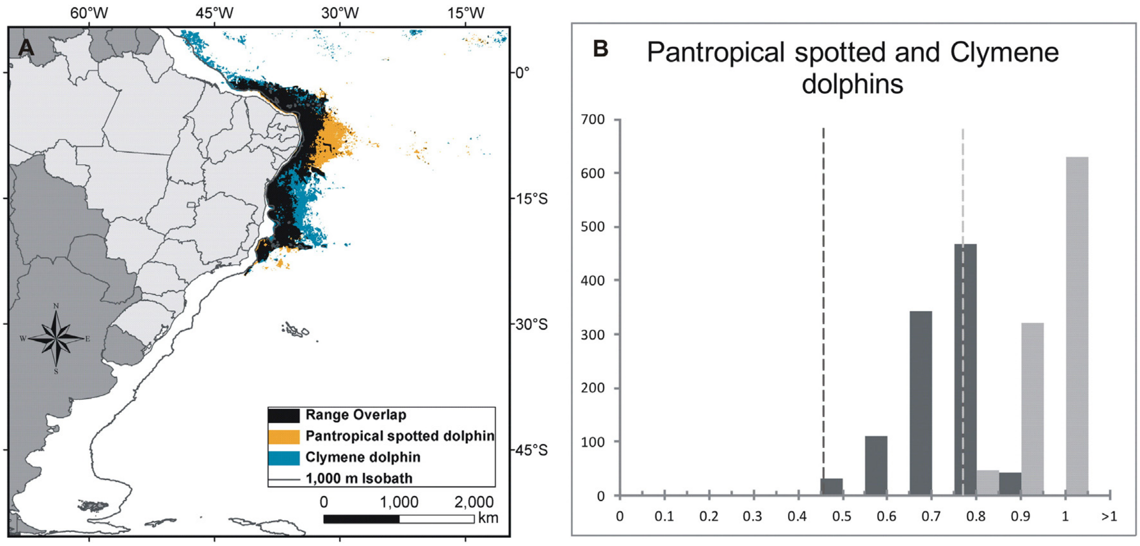

Fig. 7. A) Overlap map of potential distribution of pantropical spotted dolphin (*S. attenuata*) and Clymene dolphin (*S. clymene*) in the SWA. B) Results of the pairwise identity test between the two species. Dashed lines indicate the real calculated niche overlap obtained in ENMtools' niche overlap test (dark gray dashed lines: D = 0.453; light gray dashed lines: I = 0.763). Columns represent the niche overlap values created in the 1000 replicates of identity test (dark gray column: D = 0.689 ± .080; light gray column: I = 0.902 ± 0.0503). The true calculated overlap values (I and D) are far outside the 99.9% confidence intervals of the identity test results and thus highly significant.

requirements and spatial separation with narrow contact zones among some species in the SWA.

The analytical methods used in this study indicates that pantropical spotted dolphin, Clymene dolphin, Atlantic spotted dolphin and spinner dolphin exhibit notably contrasting environmental requirements although they seems to be sympatric. Perrin and Hohn (1994) initially proposed that both spotted dolphins were broadly sympatric in Atlantic waters. Moreno et al. (2005) suggested that these species were parapatric off the eastern coast of South American, because there are virtually no records of Atlantic spotted dolphin beyond 1000 m isobath neither records of pantropical spotted dolphin on shallow waters of the continental shelf. Instead, a narrow area of contact between both species off the coast of Rio de Janeiro was proposed (Moreno et al., 2005). The results present here agree to some extent with Moreno et al. (2005), particularly in what regards the parapatric distribution those species along the Brazilian coast, and also show that the environmental requirements of these species are highly divergent in the SWA.

In general, pantropical spotted and Clymene dolphins seem to share similar environmental constraints and may exhibit some extensive degree of overlap along their distribution as occurs in the Gulf of Mexico (Baumgartner et al., 2001; Davis et al., 1998). Both species are highly divergent regarding to Atlantic spotted dolphin as already proposed in Gulf of Mexico (Davis et al., 1998; Davis et al., 2002).

In the study conducted by Davis et al. (1998) in Gulf of Mexico and including all five *Stenella* species, the results relatives to bottom depth indicated that striped, pantropical spotted and Clymene dolphins were

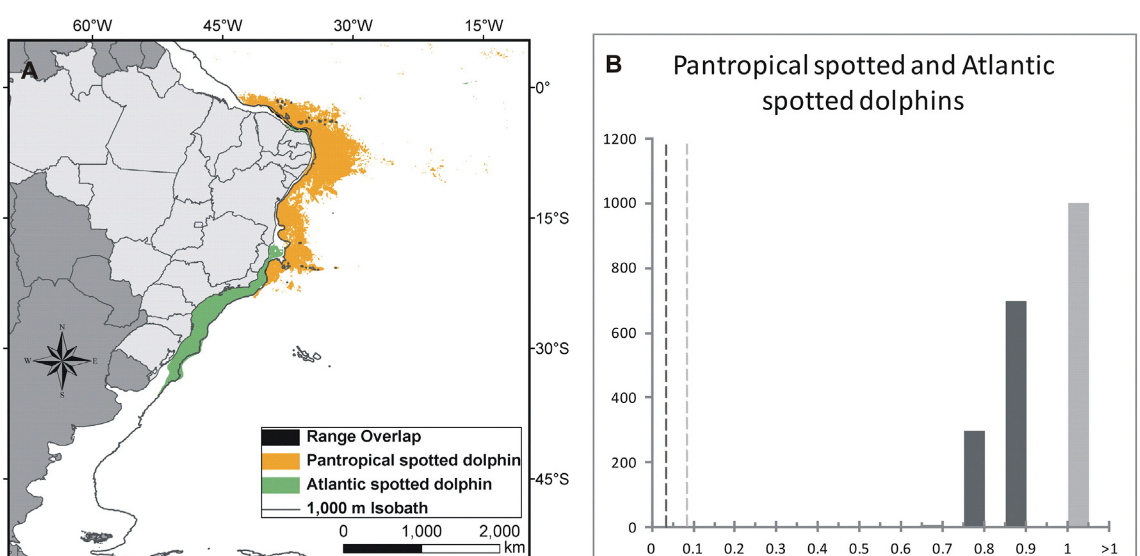

Fig. 8. A) Overlap map of potential distribution of pantropical spotted dolphin (*S. attenuata*) and Atlantic spotted dolphin (*S. frontalis*) in the SWA. B) Results of the pairwise identity test between the two species. Dashed lines indicate the real calculated niche overlap obtained in ENMtools' niche overlap test (dark gray dashed line: D = 0.033; light gray dashed line: I = 0.090). Columns represent the niche overlap values created in the 1000 replicates of identity test (dark gray column: D = 0.814 ± 0.033; light gray column: I = 0.946 ± 0.011). The true calculated overlap values (I and D) are far outside the 99.9% confidence intervals of the identity test results and thus highly significant.

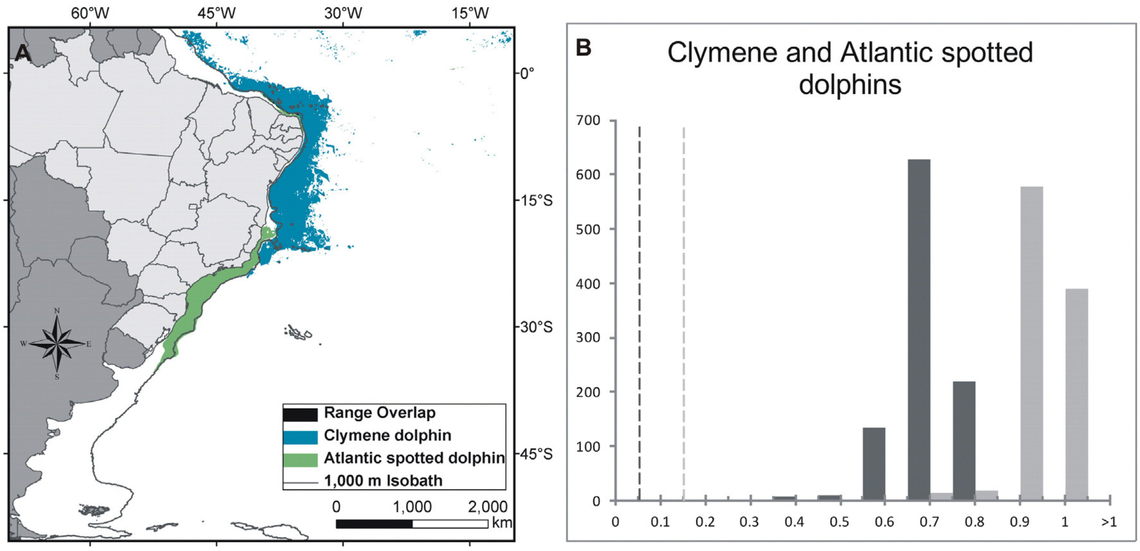

Fig. 9. A) Overlap map of potential distribution of Clymene dolphin (*S. clymene*) and Atlantic spotted dolphin (*S. frontalis*) in the SWA. B) Results of the pairwise identity test between the two species. Dashed lines indicate the real calculated niche overlap obtained in ENMtools' niche overlap test (dark gray dashed line: D = 0.051; light gray dashed line: I = 0.151). Columns represent the niche overlap values created in the 1000 replicates of identity test (dark gray column: D = 0.654 ± 0.062; light gray column: I = 0.884 ± 0.042). The true calculated overlap values (I and D) are far outside the 99.9% confidence intervals of the identity test results and thus highly significant.

found over deepest bottom depths, while Atlantic spotted dolphin was found at the shallowest bottom depths and spinner dolphin was found in intermediate values. Regarding the SST, Atlantic spotted and striped dolphins occurred in the coolest water, while pantropical spotted dolphin were found in the warmest water. The results obtained in the SWA and discussed here are similar to the study of Davis et al. (1998), except for striped dolphin that occurs in deep waters like in Meditteranean (Cañadas et al., 2002) and Japanese waters (Kasuya, 1999) and not in shallow waters as noted in the SWA. In the eastern tropical Pacific, the striped dolphins are considered an intermediate between spinner and pantropical spotted dolphins in their oceanographic preferences (Perrin et al., 1994).

Mixed-species associations between pantropical spotted and spinner dolphin is well documented in the eastern tropical Pacific (Balance et al., 2006; Norris et al., 1994; Perrin and Gilpatrick, 1994; Perrin et al., 1973) and in Hawaiian waters (Psarakos et al., 2003). In the SWA heterospecific interaction was recorded in Fernando de Noronha Island (Silva et al., 2005). Moreover, mixed groups of these species were recorded on two occasions (Fig. 10). Records of mixed groups were also made between Atlantic spotted and spinner dolphins along Brazilian continental shelf (Fig. 12). The results based on overlap maps and environmental requirements analysis suggests that the spinner dolphins exhibits intermediate environmental features in the SWA when compared with other species of *Stenella*, since is more tolerant to temperature variation like Atlantic

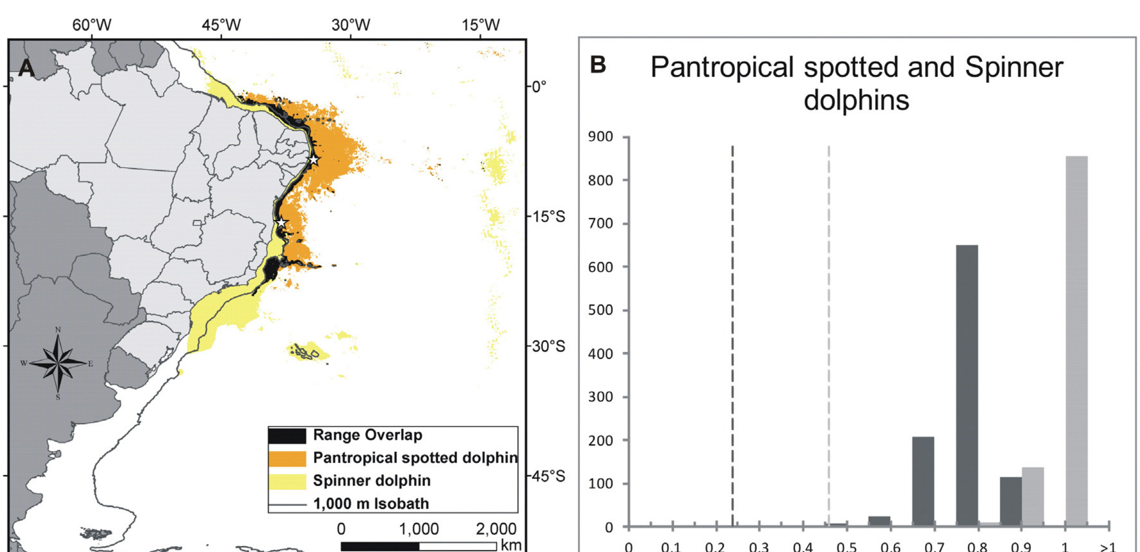

Fig. 10. A) Overlap map of potential distribution of pantropical spotted dolphin (*S. attenuata*) and spinner dolphin (*S. longirostris*) in the SWA. Star symbol indicates record of mixed groups of these species. B) Results of the pairwise identity test between the two species. Dashed lines indicate the real calculated niche overlap obtained in ENMtools' niche overlap test (dark gray dashed line: D = 0.240; light gray dashed line: I = 0.462). Columns represent the niche overlap values created in the 1000 replicates of identity test (dark gray column: D = 0.735 ± 0.061; light gray column: I = 0.926 ± 0.033). The true calculated overlap values (I and D) are far outside the 99.9% confidence intervals of the identity test results and thus highly significant.

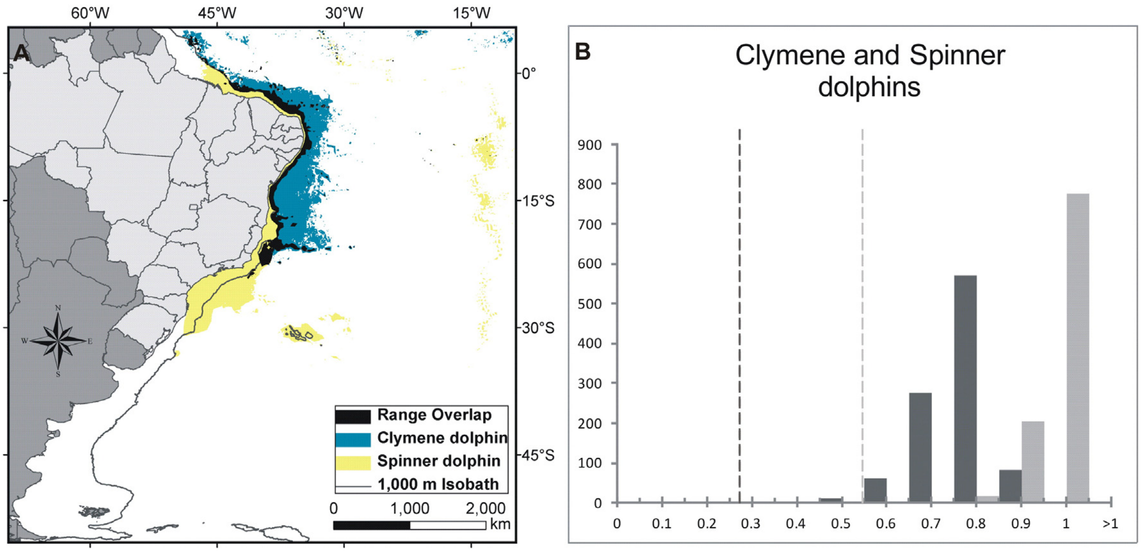

Fig. 11. A) Overlap map of potential distribution of Clymene dolphin (*S. clymene*) and spinner dolphin (*S. longirostris*) in the SWA. B) Results of the pairwise identity test between the two species. Dashed lines indicate the real calculated niche overlap obtained in ENMtools' niche overlap test (dark gray dashed line: D = 0.278; light gray dashed line: I = 0.550). Columns represent the niche overlap values created in the 1000 replicates of identity test (dark gray column: D = 0.735 ± 0.071; light gray column: I = 0.918 ± 0.039). The true calculated overlap values (I and D) are far outside the 99.9% confidence intervals of the identity test results and thus highly significant.

spotted dolphin, but does not occur in offshore oceanic waters like pantropical spotted and Clymene dolphins, with the exception of the animals that are distributed around the Archipelago of Fernando de Noronha.

Since the Moreno et al. (2005) study only Atlantic spotted dolphin has been found to have a distribution beyond the range proposed those authors: the sighting of a group of dolphins in the Abrolhos Bank (Danilewicz et al., 2013) and other in Uruguayan waters (Paro et al., 2014) that extends the distribution of the isolated southwestern Atlantic population of Atlantic spotted dolphin up to 350 km further north and up to 600 km further south, respectively. No additional observations (sightings, captures or strandings) (*e.g.* Meirelles et al., 2009; Melo et al., 2010) of any other species of *Stenella* were recorded outside the ranges proposed by Moreno et al. (2005), with the exception of the interaction of pantropical spotted dolphin with hammer head sharks recorded by Sucunza et al. (2015) few miles south of the range proposed by Moreno et al. (2005). Furthermore, the distribution suggested in this study using ecological niche modeling based solely on sightings and captures also did not predict suitable habitat beyond the known stranding records of *Stenella* in the SWA. Research effort along this area is still growing due to the rise of new marine studies centers and the subsequent increase of the number of researchers specialized in marine mammals. Unfortunately, in the SWA offshore effort has grown

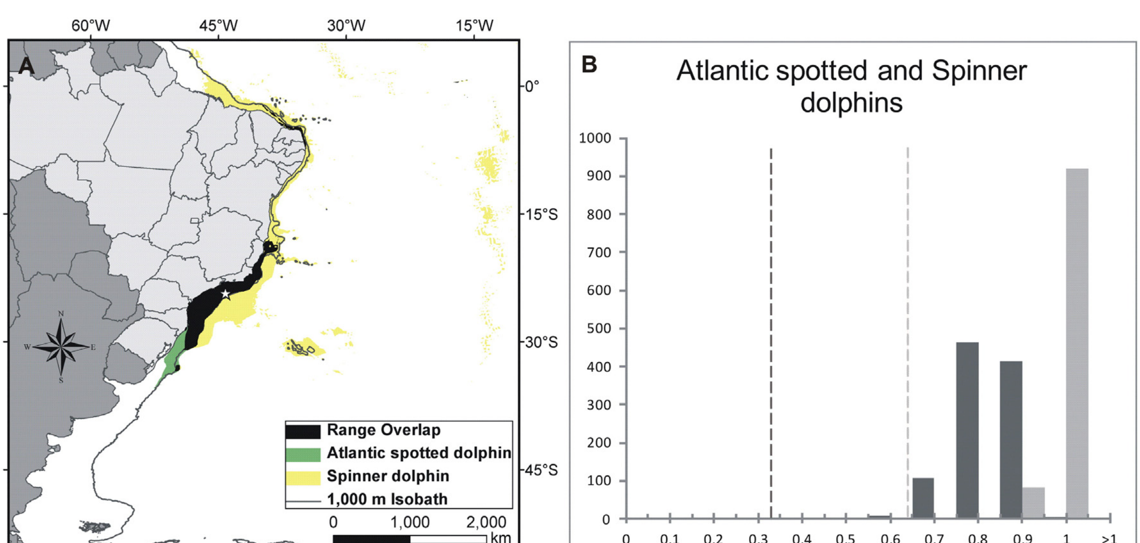

Fig. 12. A) Overlap map of potential distribution of Atlantic spotted dolphin (*Stenella frontalis*) and spinner dolphin (*S. longirostris*) in the SWA. Star symbol indicates record of mixed groups of these species. B) Results of the pairwise identity test between the two species. Dashed lines indicate the real calculated niche overlap obtained in ENMtools' niche overlap test (dark gray dashed line: D = 0.335; light gray dashed line: I = 0.646). Columns represent the niche overlap values created in the 1000 replicates of identity test (dark gray column: D = 0.778 ± 0.061; light gray column: I = 0.945 ± 0.027). The true calculated overlap values (I and D) are far outside the 99.9% confidence intervals of the identity test results and thus highly significant.

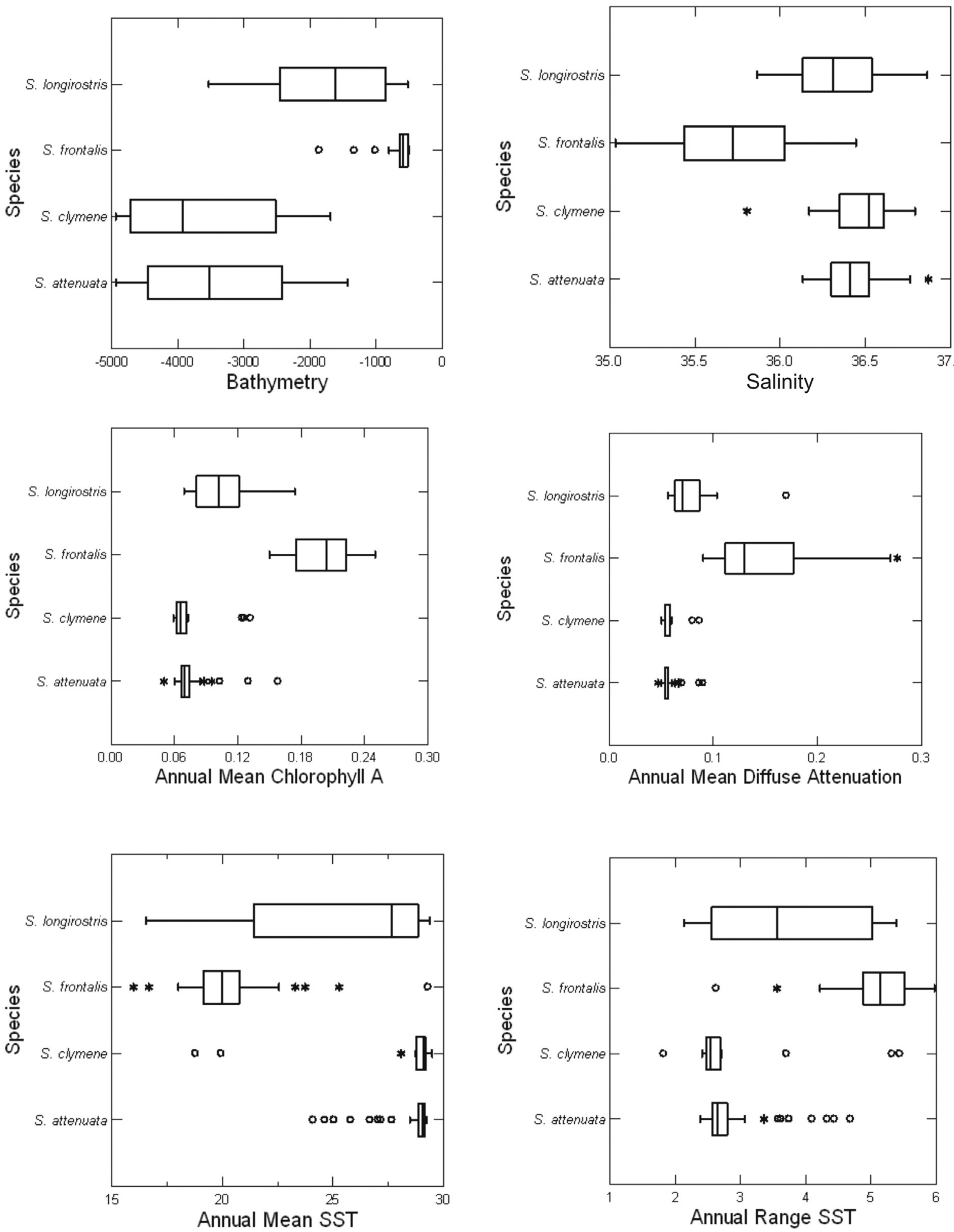

Fig. 13. Box plot of values extracted from environmental layers for each species records in the SWA. The thick vertical line inside each box represents the median; the lateral borders of the box are the 25th and 75th percentiles; the 5th and 95th percentiles are represented by the error bars; * are outliers. The results of Kruskal–Wallis test indicate that differences in the median values among the species are greater than expected by chance: bathymetry: $H = 100.33$ (p-value = 0.000); salinity: $H = 81.965$ (p-value = 0.000); annual mean of concentration of chlorophyll A: $H = 109.624$ (p-value = 0.000), annual mean of diffuse attenuation: $H = 110.152$ (p-value = 0.000); annual mean of sea surface temperature (SST): $H = 86.982$ (p-value = 0.000) and annual range of sea surface temperature (SST): $H = 87.488$ (p-value = 0.000).

at a slower pace due the lack of systematic dedicated cetacean surveys. In this sense dedicated cetacean surveys are needed to better investigate the offshore distribution proposed here.

This study demonstrated that the species distributions areas modeled by Maxent based only on sightings and captures may be close to the true distributions of the species in the SWA. This tool has great potential to address various issues such as distribution, ecology and evolution processes. Despite the difficulty of obtaining data, more studies that combine ecological niche modeling and cetaceans should be conducted.

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Author contributions

All authors have approved the final version of the manuscript. Acquisition of field data: Amaral, K. B.; Moreno, I.B.; Salvatore, S. Organization of data and compilation of literature: Amaral, K.B.; Heinzelmann, L.; Moreno, I.B. Conceived and designed the experiments: Amaral, K.B., Alvares, D.J.; Borges-Martins, M.; Moreno, I.B. Analyzed the data: Amaral, K.B., Alvares, D.J.; Borges-Martins, M.; Moreno, I.B. Contribution to writing the manuscript: Amaral, K.B., Alvares, D.J.; Borges-Martins, M.; Salvatore, S.; Moreno, I.B. Wrote the paper: Amaral, K.B.; Moreno, I.B.

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