



Original research article

## Environmental predictors of habitat suitability and biogeographical range of Franciscana dolphins (*Pontoporia blainvillei*)



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## ABSTRACT

The aim of this study was to use species distribution models to estimate the effects of environmental variables on the habitat suitability of river dolphins *Pontoporia blainvillei* (franciscanas) along their overall biogeographical distribution. Based on the literature, we selected six environmental variables to be included in the models; four climatic factors (surface sea temperature, salinity, turbidity and productivity) and two biotic factors (prey availability and fishing effort). We determined that the biographic range is under the following limits: temperature less than 19° C, a salinity of 36 psu and a minimal probability of the occurrence of fish *C. guatucupa* of 0.297. In the discussion, we postulate hypotheses on the behavioural and physiological mechanisms that cause these associations between environmental predictors and Franciscanas distribution. There was a good fit between the distribution predicted by the species distribution model and the one proposed by the experts of the International Union for Conservation of Nature; however, our analysis failed to highlight the fundamental role of bycatch as the main threat to this dolphin species.

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Species distribution models (SDMs) are associative models that relate occurrence or abundance data at known locations for individual species (distribution data) to information on the environmental characteristics of those locations. Several publications have reviewed the available SDMs (Guisan and Thuiller, 2005; Heikkinen et al., 2006; Elith and Leathwick, 2009; Cassini, 2011a, 2013). These reviews found that SDMs have been used to suitably characterise the natural distributions of species and that this information has been applied to investigate a variety of scientific and applied issues. Species distribution models have two main uses: identifying predictors or key factors of the environment that affect species distributions, or predicting distributions in new scenarios, assuming that the variables included in the model are relevant factors. When SDMs are used for the latter purpose, their output is normally a habitat suitability map that can be used in conservation and land management. The first approach has a more theoretical focus, and considers the causal drivers of species distributions.

Cassini (2011b) proposed that species distribution models can be used for ranking key factors or threats to endangered or vulnerable species. Most current ranking of threats conducted within IUCN specialist groups still relies on the subjective perspectives of workshop attendees or individual experts. Species distribution models are ideal tools for incorporating

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theoretical and mathematical rigour to the ranking threat process, because: (1) they are relatively easy and rapid to implement; (2) they can be used with different levels of knowledge about the species in question; and (3) they are particularly suitable for use at the geographical scale, for which the IUCN Red List is designed.

Most river dolphins are among the least known and most endangered of all cetaceans (Hamilton et al., 2001). They have highly disjointed geographical distributions: the Amazon River dolphin, *Inia geoffrensis*, and the Franciscana dolphin, *Pontoporia blainvillei*, are found in South America, whereas the Yangtze River dolphin, *Lipotes vexillifer*, and Indian River dolphin, *Platanista gangetica*, inhabit Asian rivers.

Of the four species of river dolphins, *P. blainvillei* is the most investigated and the only one that is distributed in the sea. These dolphins, also known as Franciscanas, inhabit shallow coastal waters of tropical and temperate regions of the western South Atlantic Ocean, from Itaúnas (18°25'S; 30°42'W), southeastern Brazil (Siciliano, 1994) to Golfo Nuevo (42°35'S; 64°48'W), Argentina (Crespo et al., 1998). They have been classified as 'vulnerable' by IUCN experts (Reeves et al., 2012 have quoted the information provided by experts in this species). Franciscanas are primarily coastal dolphins, with only occasional records of this species farther offshore than 30 m in depth (Pinedo et al., 1989; Secchi et al., 2003; Silva, 2011; Desvaux, 2013). This isobath has been used to establish the eastern border of the species' distribution by experts of the International Union for Conservation of Nature (IUCN, reviewed by Reeves et al., 2012). The South American coast of the Atlantic Ocean has wide continental platforms (Almeida et al., 2000), with a high biodiversity (Bittar and Di Benedetto, 2009; Cremer et al., 2012). The Malvinas and Brazil currents converge on this region; the first is cold and penetrates from the south and the second is from the north and is warm. This collision of currents determines that the sea in this area is very productive (Miloslavich et al., 2011).

Variables introduced in the models were:

- (1) Sea temperature: size and other functional traits of endotherms interact with environmental factors to define their thermal niche, which in turn can be translated into spatial limits of species distributions (Kearney and Porter, 2009). Taking into account the small size and the relatively thin body fat layer of this species (Rodríguez et al., 2002), low temperatures should represent a constraint to its geographic range (Mayr, 1963; William, 1983; Hind and Gurney, 1997).
- (2) Sea salinity: It has been repeatedly postulated that river dolphins cannot inhabit sea water due to osmoregulation constraints. Kamiya and Yamasaki (1974), Janech et al. (2002), Dudgeon (2000), Bräger et al. (2003), Kannan et al. (2005) and Smith et al. (2009). Although Franciscanas are the exception because they show a marine distribution, their phylogenetic origin might have imposed constraints on their adaptations for osmoregulation, thus, it is still possible that they can only inhabit areas where the salt concentration is relatively low.
- (3) Turbidity: Several authors have proposed that Franciscanas are associated with shallow waters due to their preference for turbidity (Pinedo et al., 1989; Brownell, 1989; Siciliano et al., 2002). It has been speculated that this preference for turbidity reduces the probability of encounters with predatory sharks (Norris and Dohl, 1980; Wells, 1987; Mann et al., 2000).
- (4) Ocean productivity: It has been found to be important for several species of cetaceans (Acevedo, 1991; Jaquet and Whitehead, 1996).
- (5) Fishing effort: There is a strong consensus among specialists that fishing is the main threat to Franciscanas (Reeves et al., 2012). Incidental entanglement or bycatch of these dolphins was reported repeatedly (Secchi et al., 2003; Di Benedetto and Ramos, 2001; Kinas, 2002; Dans, 2003; Bordino and Albareda, 2004; Cappozzo et al., 2007).
- (6) Prey distribution: Franciscanas prey on a wide range of fish species, however *Cynoscion guatucupa* was the most important prey for this dolphin. (Table 1). We analysed 14 studies on Franciscana's diet and we found that *C. Guatucupa* was consumed in more than 70% of the studies, and it was the most consumed prey on 13 (92.3%) studies (Table 1). Therefore, we included *C. guatucupa* distribution as a potential predictor of Franciscanas distribution in our SDM models. All the other prey species showed significantly less index of consumption (Table 1).

The aim of this study was to use SDMs to estimate the effects of environmental variables on habitat suitability and biogeographical ranges of the Franciscana, *P. blainvillei*. We selected six environmental variables to be included in the SDMs: four climatic factors (surface sea temperature, salinity, turbidity and productivity), and two biotic factors (prey availability and fishing effort). We compared the output of the SDMs with the species range proposed by the experts of the IUCN (<http://maps.iucnredlist.org/map.html?id=17978,18/3/2014>). In the following paragraphs, we explain the reasons for selecting the six environmental variables, mainly based on physiological and behavioural mechanisms that might be involved.

## 1. Methods

### 1.1. Data on Franciscana locations

As a dependent variable of the models, we used 1856 sightings and strandings that were obtained from the literature (Cremer and Simões-Lopes, 2008, Polizzi et al., 2013, Alonso et al., 2012, Bordino et al., 2004, Crespo et al., 2010, Crespo et al., 2009, Zerbini et al., 2010, Danilewicz et al., 2012, Santos et al., 2009, Bordino, 2002, Acevedo, 2002, Flores, 2009, Zerbini et al., 2011, Di Benedetto and Ramos, 2001, Bordino et al., 2013, Mendez et al., 2008, Montealegre-Quijano and Ferreira, 2010, Abud et al., 2008, Mendez, 2010, Failla et al., 2004) and from online biological databases GBIF and OBIS ([www.gbif.org](http://www.gbif.org)

**Table 1**

Results of the analyses of 14 studies on the diet of *Pontoporia blainvillei*. % studies: frequency of studies in which the species was present in the diet. Mean ranking: for each study, prey species were ranking based on their representation on dolphin diet; the mean ranking was obtained across studies. %S/MR represents the ratio between these two measurements, which represents an index of prey consumption. 21 species were not included in the list for having an index less than 1.

Species	% studies	Mean ranking	%S/MR
<i>Cynoscion guatucupa</i>	71.4	1.6	44.6
<i>Pellona harroweri</i>	28.6	2.0	14.3
<i>Trichiurus lepturus</i>	64.3	5.7	11.3
<i>Paralanchurus brasiliensis</i>	71.4	6.5	11.0
<i>Micropogonias furnieri</i>	64.3	7.0	9.2
<i>Isopisthus parvipinnis</i>	35.7	4.4	8.1
<i>Urophycis brasiliensis</i>	35.7	4.8	7.4
<i>Stellifer rastrifer</i>	42.9	6.5	6.6
<i>Macrodon ancylodon</i>	64.3	10.7	6.0
<i>Umbrina canosai</i>	42.9	7.3	5.8
<i>Anchoa filifera</i>	28.6	5.8	5.0
<i>Porichthys porosissimus</i>	42.9	8.7	4.9
<i>Cynoscion jamaicensis</i>	35.7	7.6	4.7
<i>Trachurus lathami</i>	35.7	8.8	4.1
<i>Stellifer brasiliensis</i>	21.4	6.0	3.6
<i>Doryteuthis plei</i>	7.1	2.0	3.6
<i>Gobionellus oceanicus</i>	7.1	2.0	3.6
<i>Chirocentron bleekermanus</i>	21.4	6.0	3.6
<i>Engraulis anchoita</i>	21.4	7.0	3.1
<i>Peprilus paru</i>	21.4	7.7	2.8
<i>Anchoa marini</i>	21.4	9.0	2.4
<i>Cetengraulis edentulus</i>	7.1	3.0	2.4
<i>Odonthestes argentinensis</i>	7.1	3.0	2.4
<i>Larimus breviceps</i>	28.6	12.8	2.2
<i>Stromateus brasiliensis</i>	14.3	7.5	1.9
<i>Raneya fluminensis</i>	21.4	11.7	1.8
<i>Cynoscion microlepidotus</i>	14.3	8.0	1.8
<i>Anchoviella lepidentostole</i>	21.4	13.3	1.6
<i>Opisthonema oglinum</i>	7.1	5.0	1.4
<i>Odontognathus mucronatus</i>	14.3	10.5	1.4
<i>Doryteuthis sanpaulensis</i>	7.1	6.0	1.2
<i>Leptonotus blainvillanus</i>	7.1	6.0	1.2
<i>Lycengraulis grossidens</i>	14.3	12.5	1.1
<i>Ctenosciaena gracilicirrus</i>	14.3	13.5	1.1
<i>Pomatomus saltatrix</i>	14.3	13.5	1.1

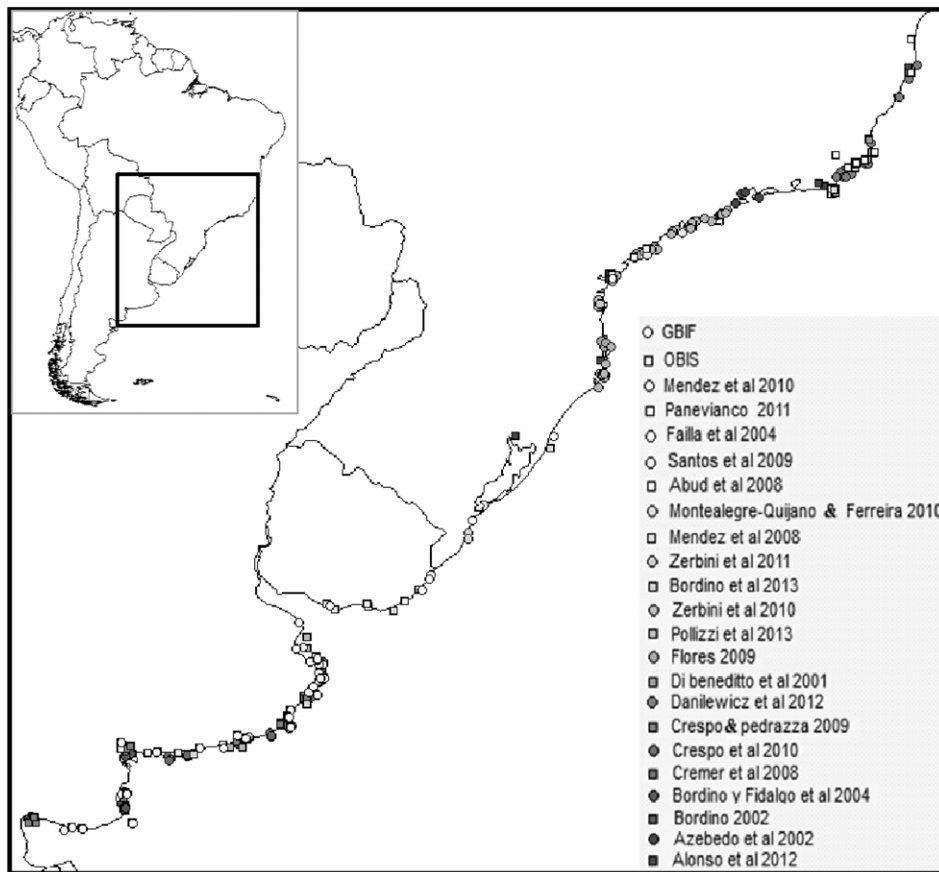
and [www.seamap.env.duke.edu](http://www.seamap.env.duke.edu)). For each sighting, we estimated values of the six environmental variables, associated by spatial coincidence. For each stranding, we assumed that the dead animal had its home range within a semi-circular buffer area of 100 km, where we estimated the mean values of the six environmental variables.

## 1.2. Environmental variables

Data on oceanographic variables were obtained from two sources: the National Aeronautics and Space Administration (NASA) of the United States and the National Commission on Space Activities (CONAE) of Argentina. Sea-surface temperature was obtained from the Active Archive Center of Distribution of Physical Oceanography (POET, <http://poet.jpl.nasa.gov/>) and from source AVHRR Pathfinder Version 5 (4 km resolution). Productivity and turbidity (Diffuse attenuation coefficient at 490 nm) were obtained by the application Giovanni (<http://disc.sci.gsfc.nasa.gov/giovanni>) and the Goddard Center for Information Services and Earth Sciences, respectively (source: Modis-Aqua, 4 km resolution). Ocean salinity was obtained from the database of the CONAE SAC-D Aquarius satellite, the first to obtain sea-surface salinity. For each  $0.5^\circ \times 0.5^\circ$  cell of the grid, mean values of these four variables (temperature, productivity, turbidity, salinity) were obtained from the data available for year 2012.

Data on fisheries were obtained from maps published by Stewart et al. (2010). These created a comprehensive database of fishing effort metrics and the corresponding spatial limits of fisheries and map fishing effort density (measured as boat-metres per km<sup>2</sup>) in the coastal zones of six ocean regions, using a spatial resolution of 1 km<sup>2</sup>.

Data on the distribution of the fish *C. guatucupa* were obtained from Fishbase ([www.fishbase.org](http://www.fishbase.org)), a widely recognised database that is linked to OBIS ([www.iobis.org](http://www.iobis.org)) and GBIF ([www.gbif.org](http://www.gbif.org)) (Costello and Vanden Berghe, 2006; Berghe et al., 2010; Jochum and Huettmann, 2010; Bluhm et al., 2010; Tsikliras et al., 2013). The expected distribution of *C. guatucupa* throughout the Franciscanas' range was obtained using SDMs with four variables (sea surface temperature, productivity, bathymetry, and sea surface salinity), following a protocol described in the following section, which was analogous to that used for dolphins. The application of SDMs is common for fishes (Valavanis et al., 2008; Labay et al., 2011; Lenoir et al., 2011 and Monk et al., 2012).



**Fig. 1.** Study area and data for 1855 sightings and stranding of Franciscanas used as presences in the species distribution models. One data set ( $-30.70S$ ,  $-18.35W$ ) was not included in the map because it decreased map resolution.

### 1.3. Species distribution models

We tested three SDMs that used presence-only data: the Maximum Entropy Model (MaxEnt), Environmental Niche Factor Analysis (ENFA) and Bioclim (based on climatic envelopes) (see Fig. 1). Accuracy assessment for each model was measured using two different indices: the area under the curve (AUC) from the receiver operating characteristic curve (ROC, Woodward, 1999) and Cohen's Kappa index (Cohen, 1960). The ROC curve is the relationship between the sensitivity and the false positive fraction. The AUC is the area under the ROC curve, with a value of 0.5 representing a random model, values between 0.8 and 0.9 representing models with a good fit and values over 0.9 being an excellent fit (Manel et al., 2001; Thuiller, 2003). The Kappa statistic defines the accuracy of prediction, relative to the accuracy that might have resulted by chance alone; it ranges from  $-1$  to  $+1$ , where  $+1$  indicates perfect agreement between predictions and observations and values of 0 or less indicate agreement no better than random classification. These two indices are commonly used to compare several types of models (Fielding and Bell, 1997; Pearce and Ferrier, 2000; Miller and Franklin, 2002; Brotons et al., 2004) but cannot be strictly applied to ENFA and BIOCLIM, because no absence data are used as input in the models. Thus, following the methods of Brotons et al. (2004), the predictive results of ENFA-BIOCLIM were applied for a range of cut-off values (0–100) to the presence and pseudo-absence data set used to fit MaxEnt models and produce comparable indices. The Jackknife test was used to determine the weight of each variable within each model. This test generates a model with each variable separately and also creates another set of models, which excludes one of the variables. For each model, the AUC and Kappa indices are measured (Phillips et al., 2004; Elith et al., 2011).

The MaxEnt technique has its roots in information theory and is a statistical modelling method in several fields that has been widely used as a type of SDM (Elith et al., 2006; Phillips et al., 2006). We used the MaxEnt program ([www.cs.princeton.edu/~schapire/maxent](http://www.cs.princeton.edu/~schapire/maxent)) as described in detail in Phillips et al. (2006), which employs a maximum likelihood method that models species distributions by generating a probability distribution over the pixels in a grid of the study area. MaxEnt estimates a probability distribution that maximises entropy (i.e., that is the closest to uniform), subject to a set of constraints derived from measurements of assumed suitable habitat values at species occurrence locations. For MaxEnt analysis, we used a Java environment to generate a SWD file for presence data and a package of dependent variables in ASCII format. We used the following settings of MaxEnt v.3.3.2: automatic feature selection, a regularisation multiplier

at unity, a maximum of 500 iterations, 10 replicates and a convergence threshold of 10<sup>-5</sup>. We also used a random test percentage of 10%. A total of 100 pseudo-absences were randomised in the study area for the construction of the confusion matrix. A map of the potential distribution of the species was constructed using the logistic output (Phillips and Dudik, 2008).

A modified principal components analysis is used by ENFA to develop a model based on occurrence-only data (Hirzel et al., 2002). The observed environment is compared to the background data of the study area and the analysis produces factors similar to a principal components analysis. Model projection uses the geomeans method of Hirzel and Arlettaz (2003). Analyses using ENFA were performed using the BIOMAPPER software (<http://www2.unil.ch/biomapper/index.html>). A MacArthur's broken-stick distribution analysis was used to establish factor significance (Hirzel et al., 2002). Distance geometric-mean algorithms were used for habitat suitability computations (Hirzel and Arlettaz, 2003). These algorithms make no assumption about the shape of the species distribution. The geometric mean produces a smooth set of envelopes around the observation points and provides a good generalisation of the niche (Hirzel and Arlettaz, 2003).

BIOCLIM uses the mean and standard deviation of each environmental variable separately to calculate bioclimatic envelopes (Busby, 1991). For each given variable, the algorithm calculates these two parameters (assuming normal distribution) for each point of occurrence (in these case, centroids). Each variable has its own envelope represented by the interval  $[m - c \times s, m + c \times s]$ , where  $m$  is the mean,  $c$  is the cut-off input parameter, and  $s$  is the standard deviation. Besides the envelope, each environmental variable has additional upper and lower limits taken from the maximum and minimum values related to the set of occurrence (Nix, 1986). For BIOCLIM analysis, we used DIVA-GIS software (version 7.1.7, [www.diva-gis.org](http://www.diva-gis.org)) and the modelling module, with the option to run the model BIOCLIM.

The SDMs were applied to obtain probability distributions of the fish *C. guatucupa*, the most-used and preferred prey of Franciscanas throughout their range. The MaxEnt model showed a higher AUC (AUC = 0.888, SD = 0.010) than ENFA (AUC = 0.623, SD = 0.008) and BIOCLIM (AUC = 0.700, SD = 0.010), and was the only model to meet the criterion of an AUC > 0.8. Thus, the probability distribution generated by MaxEnt was used as one of the six variables to model the distribution of Franciscanas.

## 2. Results

When applied to Franciscana training data, the MaxEnt model had a better fit to data according to the ROC curve and Kappa index (AUC = 0.978, SD = 0.009; Kappa = 0.798, SD = 0.052) than ENFA (AUC = 0.665, SD = 0.018; Kappa = 0.522, SD = 0.061) or BIOCLIM (AUC = 0.343, SD = 0.080; Kappa = 0.398, SD = 0.001). Taking into account the contribution of each variable separately, and according to both AUC and Kappa methods, there were three predictors of dolphin distribution (Fig. 2). The potential distribution of the fish species *C. guatucupa* represented the most important variable (percent contribution: 44.3%), followed by two physical variables; temperature (24%) and salinity (21.3%).

The edges of the expected distribution map produced by MaxEnt showed three salient features (Fig. 3). The southern edge of the distribution followed the shape of the isotherms, which is distorted by the effect of the Malvinas Current that transports cold water to lower latitudes close to the coast. Analogously, the northern edge followed the form of the saline fronts. The eastern edge showed an expansion into ocean waters at the level of the mouth of the De la Plata River, which is associated with a similar expansion in the distribution probabilities of the Franciscanas' main prey.

The quantitative limits of physical factors can be established by comparing the map of distribution probabilities of Franciscanas, and those obtained for the four main predictors (Fig. 3): southwards, 18.9 and 20.4 °C isotherms; northwards, a salinity of 36 psu; and eastwards, a minimal probability of occurrence of *C. guatucupa* of 0.297.

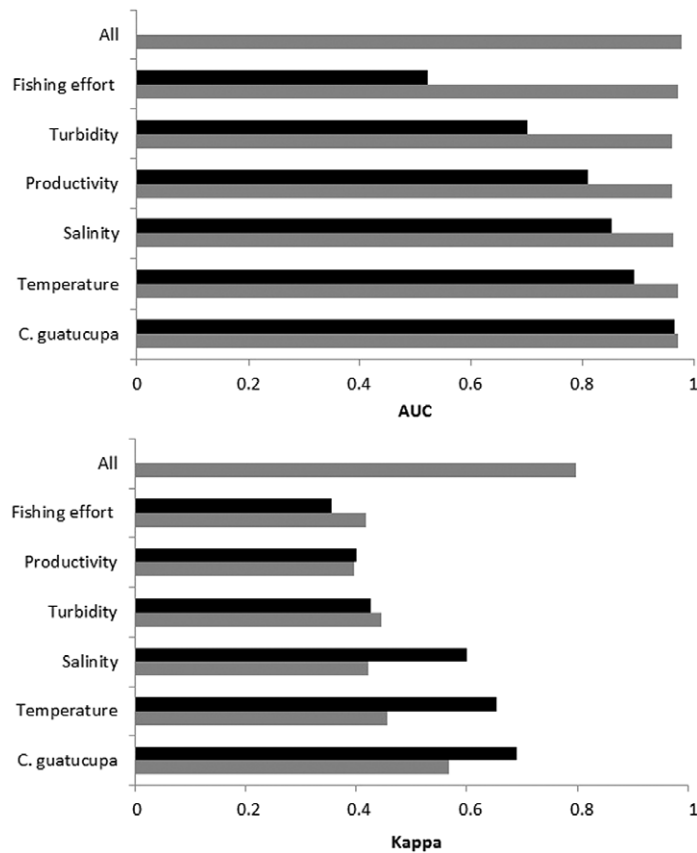
There was a close agreement between the shape of the overall biogeographic distribution obtained with MaxEnt and with that produced by the experts of the IUCN (Fig. 4). The SDM was even able to capture discontinuities in the distribution proposed by the experts for the Northern portion of the Franciscanas' distribution.

## 3. Discussion

### 3.1. Predictors and their mechanisms

Low temperatures appeared to be a relevant factor that precludes the expansion of the distribution range of Franciscanas to the southern waters of the Patagonian coast. To obtain a preliminary estimate of the lower critical temperature for Franciscanas, we applied the cylindrical model of heat loss, modified by Watts et al. (1993). The critical temperatures obtained using this simple model were 18.9 and 20.4 °C, depending on minimal and maximal lengths/weights, which approximately agree with the value of the isotherm that was observed, which accompanied the southern border of the Franciscanas' range. This result, although very preliminary, suggests that thermoregulation limitations might be a mechanism involved in delineating the southern range of this dolphin.

Salinity appeared to be a significant variable for delineating the shape of the northern and northeastern borders that follow the salinity fronts. Due to its small body size, the absolute size of the Pontoporia's kidney is among the smallest of all marine mammal species, including pinnipeds (Kamiya and Yamasaki, 1974; Beuchat, 1996). The Franciscana dolphin appears to be physiologically adapted to live in the sea and tolerate certain salinity levels. However, some functional limitations due



**Fig. 2.** Jackknife test on AUC values and Kappa test of the MaxEnt model applied to Franciscanas (*Pontoporia blainvillei*). The most important variables were prey distribution, temperature and salinity, in that order. For each variable the black bar corresponds to models generated with only this variable. The grey bars correspond to the generated models without one of the variables.

to kidney size or on the structure of nephrons could explain why salt concentration is a relevant factor that determines habitat suitability. Unfortunately, we did not find literature that compared the structure of nephrons of Franciscanas to other dolphin species.

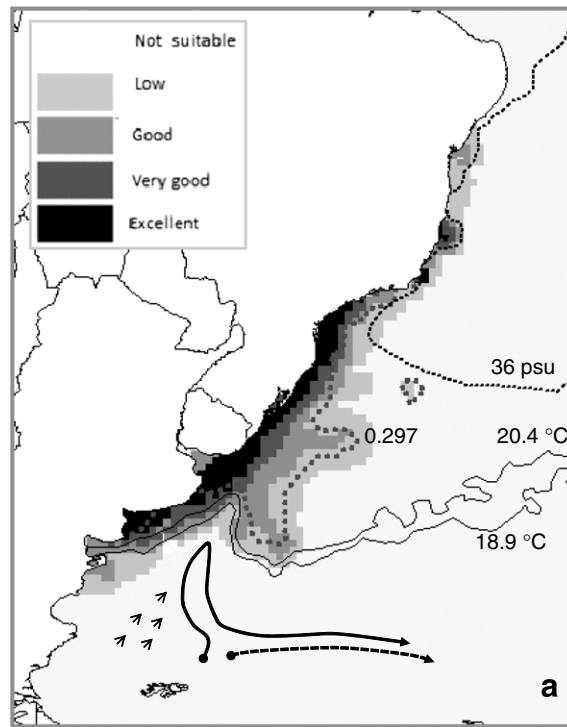
As expected, the distribution of Franciscanas was positively related to the distribution of its main prey, *C. guatucupa*. The availability of prey species over areas of different relief has been described as a major factor influencing the distribution patterns in dolphins (Hui, 1974), and several species show this trend (Reilly, 1990; Gowans and Whitehead, 1995; Heithaus and Dill, 2002; Benoit-Bird and Au, 2003; Moreno, 2005; Doksaeter et al., 2008; Viddi et al., 2010). Because the distribution of *C. guatucupa* was itself predicted by a model, this creates a potential problem of dependence among variables. This problem is improbable in this specific case, because the distribution of this prey was dependent on several variables, and the predictor introduced into the final model (i.e. MaxEnt results obtained with *C. guatucupa*) was the product of the complex mathematical relationships among variables.

Our study did not find support for previous statements that turbidity could be an important ocean determinant of *Pontoporia* distribution. One possible explanation is provided by Danilewicz et al. (2009), who reviewed the literature on the relationship between water turbidity and shark predation risk in dolphins, and concluded that the link is not a completely understood and might instead, be complex and highly variable geographically. Moreover, they suggested that depending on the shark predation behaviour, coastal turbid waters might represent a more dangerous habitat than translucent pelagic waters.

We did not find a significant relationship between Franciscanas and fishery distribution. We might have failed to detect a relationship because our analyses were based on an inappropriate measure of fishing effort. Another possibility is that incidental entanglement operates at a local scale and is therefore not expected to shape the distribution at larger ecological scales. This possibility will be further discussed in the last section of this Discussion.

### 3.2. Multiple predictors or selected factors

We incorporated only a restricted number of environmental factors into the SDMs, which were selected based on previous information that suggested the types of effects that these potential determinants might have on habitat suitability and



**Fig. 3.** Distribution of habitat suitability in accordance to MaxEnt model (grey scale). The shape of the expected southern border appears to be modulated by the cold water front of the Malvinas current. The 20.4 °C and 18.9 °C isotherms (dotted lines at the bottom) form the southern limit of the *Pontoporia* distribution. To the north and northeast, the shape of the distribution of habitat suitabilities takes three form of the 36 psu salinity front (dotted line on the top). The minimum training probability line (dotted line with the value 0.297) of the estimated distribution of *C. guatucupa* forms the eastern edge of the Franciscanas distribution. The grey solid line represents the Malvinas Current and the small arrows represent minor currents. The dashed line below the Malvinas Current represents the Antarctic Circumpolar Current. The thresholds of the legend correspond to the names and default values provided by the software DIVAGIS for model outputs: Not suitable, Low (0–2.5 percentile), Good (2.5–5 percentile), Very good (5–10 percentile), Excellent (10–20 and 20–36 percentiles, together). The last two categories provided by DIVAGIS (Very high and Excellent) merged into a single category, Excellent, for better visualisation of the results.

the biogeographical distribution of Franciscanas. Furthermore, we postulated hypotheses on the possible physiological or behavioural mechanisms involved.

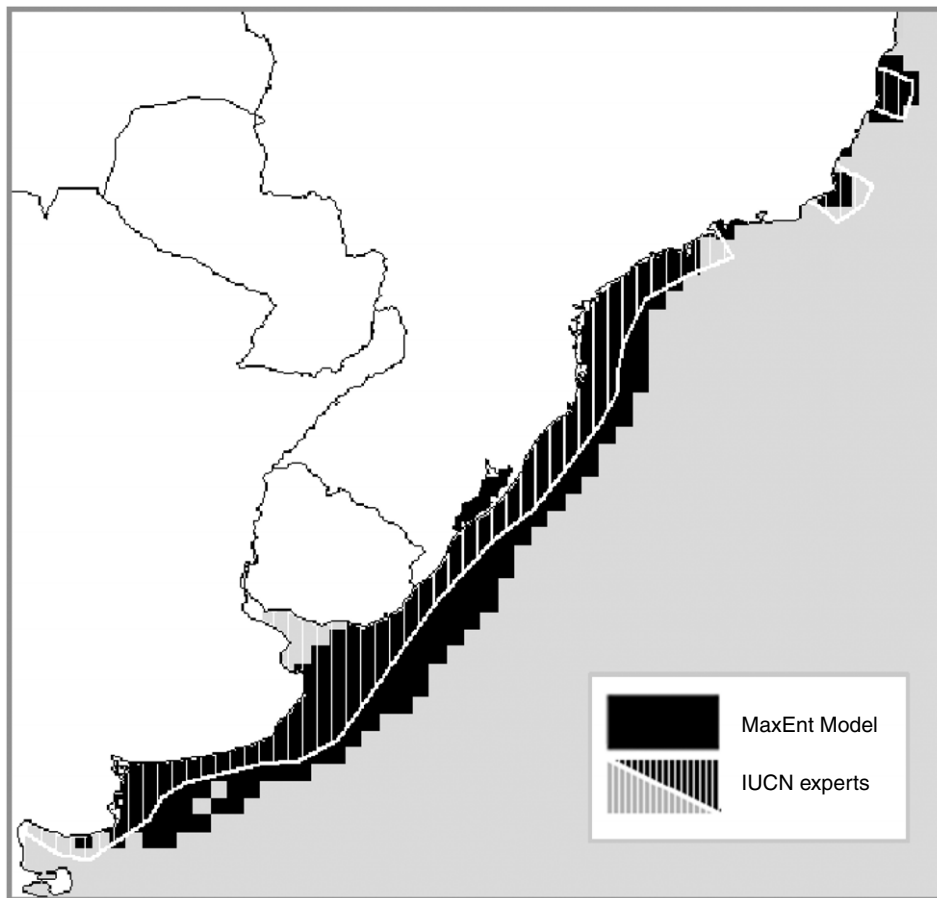
Most SDMs are based on correlation statistics, from which causation cannot strictly be inferred, but summing correlative results based on ecologically meaningful predictors can provide support to an hypothesis (Cassini, 2011a). Many SDM studies include a large amount of candidate predictors, motivated by the availability of data sets, the friendly presentation of statistical packages, and a belief that the model will identify those variables that are important predictors (Elith and Leathwick, 2009).

In contrast to this approach, some modellers have argued that the success of SDMs in explaining the distribution of habitat suitability depends on the correct selection of the environmental variables introduced into the models (e.g., McNally, 2000). Carefully selecting predictors can reduce these negative effects, with the additional advantage of generating hypotheses concerning the factors that determine the distribution, leading to more explanatory and less descriptive models. In this study, we followed the second approach, expecting to improve model predictability.

### 3.3. Relevance to conservation

We obtained a good fit between the map obtained with the MaxEnt model and the map produced by the IUCN experts. There are some discrepancies in La Plata Estuary and also in the frontiers of the distribution. This result supports the contention that SDMs can facilitate the work within IUCN Specialist Groups and other similar types of organisations (Cassini, 2013). It is important to mention that whereas IUCN experts used the 30-m isobath to establish the eastern border of their distribution, we did not use bathymetry as a predictor. This difference is important because it means that although the border of the distribution in the first map was built inductively, in the second map, it was deduced from key predictors.

Translating the results for the main environmental predictors into a ranking of future threats, our results suggest that fishery might have a potential influence on habitat suitability if it impacts on stocks of preferred prey, such as *C. guatucupa*. Climate change is another relevant impact because it can influence both temperature and salinity. If global warming implies an increment in sea temperature and a decrement in sea salinity, the expectation is of an increment in the biogeographical range of this dolphin species. These are very preliminary hypotheses based on a simple associative analysis.



**Fig. 4.** Comparison between the map produced by the experts of the International Union for Conservation of Nature (Reeves et al., 2012) and the map produced by a species distribution model ('excellent' and 'very good' suitabilities in Fig. 3) for Franciscanas (*Pontoporia blainvillei*). There is a closed agreement between maps.

We did not find an effect of fishery on habitat suitability, although it is well established that by-catch is the main threat for this species. This lack of sensitivity in our analysis is a major limitation of this study. At present, there is much information available on Franciscanas, with detailed information on local populations in Brazil and Argentina. Due to the scale of our analysis, it is impractical to take into account all the details provided by these studies. To disentangle the effects of different environmental factors at a biogeographical scale, it is unavoidably necessary to sacrifice precision at a local scale. In the specific case of fishery, we used a global database that clearly is unable to capture the complexity of the different gear traditions used in different regions, or seasonal variations in fishing pressure, and many other relevant factors that might influence dolphin mortality at a local scale.

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### References

- Abud, C., Costa, P., Dimitriadis, C., Franco, V., Laporta, P., Passadore, C., Szephegyi, M., 2008. Final Report for The Rufford Small Grants Foundation.
- Acevedo, A., 1991. Behaviour and movements of bottlenose dolphins, *Tursiops truncatus*. *Aquatic Mammals* 17, 137–147.
- Almeida, F.F.M.D., Brito Neves, B.B.D., Dal Ré Carneiro, C., 2000. The origin and evolution of the South American Platform. *Earth-Sci. Rev.* 50 (1), 77–111.
- Alonso, M.B., Eljarrat, E., Gorga, M., Secchi, E.R., Bassoi, M., Barbosa, L., Barceló, D., 2012. Natural and anthropogenically-produced brominated compounds in endemic dolphins from Western South Atlantic: another risk to a vulnerable species. *Environ. Pollut.* 170, 152–160.
- Benoit-Bird, K.J., Au, W.W.L., 2003. Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. *Behav. Ecol. Sociobiol.* 53 (6), 364–373.
- Berghe, E.V., Stocks, K.I., Grassle, J.F., 2010. Data integration: the ocean biogeographic information system. In: *Life in the World's Oceans: Diversity, Distribution, and Abundance*, Vol. 20. pp. 333–353.
- Beuchat, A.C., 1996. Structure and concentrating ability of the mammalian kidney: correlations with habitat. *Am. J. Physiol.—Regul. Integr. Compar. Physiol.* 271, 157–179.



- Bittar, V.T., Di Benedetto, A.P., 2009. Diet and potential feeding overlap between *Trichiurus lepturus* (Osteichthyes: Perciformes) and *Pontoporia blainvillei* (Mammalia: Cetacea) in northern Rio de Janeiro, Brazil. *Zoology* 26 (2), 374–378.
- Bluhm, B., Watts, D., Huettmann, F., 2010. Free database availability, metadata and the Internet: an example of two high latitude components of the census of marine life. In: *Spatial Complexity, Informatics, and Wildlife Conservation*. Springer, Japan, pp. 233–243.
- Bordino, P., 2002. *Pontoporia* sightings.
- Bordino, P., Albareda, D., 2004. Incidental mortality of Franciscana dolphin (*Pontoporia blainvillei*) in coastal gillnet fisheries in Northern Buenos Aires, Argentina. In: *International Whaling Commission Meeting*, Sorrento, Italy.
- Bordino, P., Albareda, D., Fidalgo, G., 2004. Abundance estimation of Franciscana dolphin (*Pontoporia blainvillei*) from boat surveys in Buenos Aires, Argentina. In: *Technical Paper SC56/SM13*. 56th IWC Meeting, Sorrento, Italy.
- Bordino, P., Mackay, A.I., Werner, T.B., Northridge, S.P., Read, A.J., 2013. Franciscana bycatch is not reduced by acoustically reflective or physically stiffened gillnets. *Endangered Species Res.* 19.
- Bräger, S., Harraway, J.A., Manly, B.F.J., 2003. Habitat selection in a coastal dolphin species (*Cephalorhynchus hectori*). *Mar. Biol.* 143 (2), 233–244.
- Brotions, L., Thuiller, W., Araújo, M.B., Hirzel, A.H., 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography* 27, 437–448.
- Brownell, J.R.L., 1989. Franciscana *Pontoporia blainvillei*. In: *Ridgway, S.H., Harrison, R. (Eds.), Handbook of Marine Mammals: River Dolphins and the Larger Toothed Whales*. Academic Press, pp. 45–68.
- Busby, J., 1991. BIOCLIM—a bioclimate analysis and prediction system. In: *Margules, C.R., Austin, M.P. (Eds.), Nature Conservation: Cost Effective Biological Surveys and Data Analysis*. CSIRO, Melbourne, pp. 64–68.
- Cappozzo, H.L., Negri, M.F., Pérez, F.H., Albareda, D., Monzón, F., Corcuera, J.F., 2007. Incidental mortality of Franciscana dolphin (*Pontoporia blainvillei*) in Argentina. *LAJAM* 6 (2), 127–137.
- Cassini, M.H., 2011a. Ecological principles of species distribution models: the habitat matching law. *J. Biogeogr.* 38, 2057–2065.
- Cassini, M.H., 2011b. Ranking threats using species distribution models in the IUCN Red List assessment process. *Biodivers. Conserv.* 20 (14), 3689–3692.
- Cassini, M.H., 2013. *Distribution Ecology: From Individual Habitat Use to Species Biogeographical Range*. Springer, New York, p. 321.
- Cohen, J., 1960. A coefficient of agreement for nominal scales. *Educ. Psychol. Meas.* 20, 37–46.
- Costello, M.J., Vanden Berghe, E., 2006. 'Ocean biodiversity informatics': a new era in marine biology research and management. *Mar. Ecol. Prog. Ser.*
- Cremer, M.J., Pinheiro, P.C., Simões-Lopes, P.C., 2012. Prey consumed by Guiana dolphin *Sotalia guianensis* (Cetacea, Delphinidae) and franciscana dolphin *Pontoporia blainvillei* (Cetacea, Pontoporiidae) in an estuarine environment in southern Brazil. *Série Zool.* 102 (2), 131–137.
- Cremer, M.J., Simões-Lopes, P.C., 2008. Distribution, abundance and density estimates of franciscanas, *Pontoporia blainvillei* (Cetacea: Pontoporiidae), in Babitonga bay, southern Brazil. *Rev. Bras. Zool.* 25 (3), 397–402.
- Crespo, E.A., Harris, G., Gonzales, R., 1998. Group size and distributional range of the Franciscana, *Pontoporia blainvillei*. *Mar. Mam. Sci.* 14 (4), 845–849.
- Crespo, E.A., Pedraza, S.N., Grandi, M.F., Dans, S.L., Garaffo, G.V., 2010. Abundance and distribution of endangered Franciscana dolphins in Argentine waters and conservation implications. *Mar. Mam. Sci.* 26 (1), 17–35.
- Danilewicz, D., Secchi, E.R., Ott, P.H., Moreno, I.B., Bassoi, M., Borges-Martins, M., 2009. Habitat use patterns of franciscana dolphins (*Pontoporia blainvillei*) off southern Brazil in relation to water depth. *J. Mar. Biol. Assoc. UK* 89 (5), 943–949.
- Danilewicz, D., Zerbin, A.N., Andriolo, A., Secchi, E.R., Sucunza, F., Ferreira, E., Denuncio, P., Flores, P.A., 2012. Abundance and distribution of an isolated population of franciscana dolphins (*Pontoporia blainvillei*) in southeastern Brazil: red alert for FMA? *SC/64/SM17*.
- Dans, S.L., 2003. Incidental catch of dolphins in trawling fisheries off patagonia, Argentina: can populations persist? *Ecol. Appl.* 13, 754–762.
- Desvieux, J.A.S., 2013. Captura accidental da Toninha, *Pontoporia blainvillei* (Cetacea: Pontoporiidae) e do boto-cinza, *Sotalia guianensis* (Cetacea: Delphinidae) em redes de pesca no complexo estuarino lagunar de Cananéia, litoral sul do estado de São Paulo.
- Di Benedetto, A.P.M., Ramos, R.M.A., 2001. Biology and conservation of the Franciscana (*Pontoporia blainvillei*) in the north of Rio de Janeiro State, Brazil. *Ana. J. Cetacean Res. Manag.* 3 (2), 185–192.
- Doksæter, L., Olsen, E., Nøttestad, L., Fernø, A., 2008. Distribution and feeding ecology of dolphins along the Mid-Atlantic Ridge between Iceland and the Azores. *Deep Sea Res. Part II* 55 (1), 243–253.
- Dudgeon, D., 2000. Conservation of freshwater biodiversity in Oriental Asia: constraints, conflicts, and challenges to science and sustainability. *Limnology* 1 (3), 237–243.
- Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettman, F., Leathwick, J.R., Lehmann, A., Li, J., Lohman, L.G., Loisell, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M.C., Peterson, A.T., Phillips, S.J., Richardson, K.S., Scachetti Pereira, R., Schapire, R.E., Soberon, J., Williams, S., Wis, M.S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29 (2), 129–151.
- Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* 40, 677–697.
- Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* 17 (1), 43–57.
- Failla, M., Iñiguez, M.A., Tossenberger, V., de Haro, C., 2004. Bioecology of Franciscana (*Pontoporia blainvillei*) in Northern Patagonia, Argentina. In: *Report SC/56/SM24* 56th Annual Meeting of the Scientific Committee of the International Whaling Commission, Sorrento, Italy.
- Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24 (1), 38–49.
- Flores, P.A., 2009. Occurrence of franciscana (*Pontoporia blainvillei*) in Baía Norte, southern Brazil. *LAJAM* 7 (1–2), 93–95.
- Gowans, S., Whitehead, H., 1995. Distribution and habitat partitioning by small odontocetes in the Gully, a submarine canyon on the Scotian Shelf. *Can. J. Zool.* 73, 1599–1608.
- Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* 8, 993–1009.
- Hamilton, H., Caballero, S., Collins, A.G., Brownell, R.L., 2001. Evolution of river dolphins. *Proc. R. Soc. Lond. B Biol. Sci.* 268 (1466), 549–556.
- Heikkinen, R.K., et al., 2006. Methods and uncertainties in bioclimatic envelope modeling under climate change. *Prog. Phys. Geogr.* 30, 751–777.
- Heithaus, M.R., Dill, L.M., 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology* 83 (2), 480–491.
- Hind, A.T., Gurney, W.S., 1997. The metabolic cost of swimming in marine homeotherms. *J. Exp. Biol.* 200 (3), 531–542.
- Hirzel, A.H., Arlettaz, R., 2003. Modeling habitat suitability for complex species distributions by environmental-distance geometric mean. *J. Environ. Manag.* 32 (5), 614–623.
- Hirzel, A.H., Hausser, J., Chessel, D., Perrin, N., 2002. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology* 83 (7), 2027–2036.
- Hui, C.A., 1974. Undersea topography and distribution of dolphins of the genus *delphinus* in the southern California bight. *J. Mammal.* 60 (3), 521–527.
- Janech, M.G., Chen, R., Klein, J., Nowak, M.W., McFee, W., Paul, R.V., Fitzgibbon, W., Ploth, D.W., 2002. Molecular and functional characterization of a urea transporter from the kidney of a short-finned pilot whale. *Am. J. Physiol.—Regul. Integr. Compar. Physiol.* 282 (5), R1490–R1500.
- Jaquet, N., Whitehead, H., 1996. Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. *Marine Ecol. Prog. Ser.* 135 (1), 1–9.
- Jochum, K., Huettmann, F., 2010. Spatial information management in wildlife ecology: adding spatially explicit behaviour data to the equation? In: *Spatial Complexity, Informatics, and Wildlife Conservation*. Springer, Japan, pp. 175–191.
- Kamiya, T., Yamasaki, F., 1974. Organ weights of *Pontoporia blainvillei* and *Platanista gangetica* (Platanistidae). *Sci. Rep. Whales Res. Inst.* 26, 265–270.
- Kannan, K., Ramu, K., Kajiwara, N., Sinha, R.K., Tanabe, S., 2005. Organochlorine pesticides, polychlorinated biphenyls, and polybrominated diphenyl ethers in Irrawaddy dolphins from India. *Arch. Environ. Contam. Toxicol.* 49 (3), 415–420.
- Kearney, M., Porter, W.P., 2009. Size, shape, and the thermal niche of endotherms. *Proc. Natl. Acad. Sci. USA* 106 (Suppl 2), 19666–19672.
- Kinas, P.G., 2002. The impact of incidental kills by gill nets on the Franciscana dolphin (*Pontoporia blainvillei*) in southern Brazil. *Bull. Mar. Sci.* 70 (2), 409–421.

- Labay, B., Cohen, A.E., Sissel, B., Hendrickson, D.A., Martin, F.D., Sarkar, S., 2011. Assessing historical fish community composition using surveys, historical collection data, and species distribution models. *PLoS One* 6 (9), e25145.
- Lenoir, S., Beaugrand, G., Lecuyer, E., 2011. Modeled spatial distribution of marine fish and projected modifications in the North Atlantic Ocean. *Global Change Biol.* 17 (1), 115–129.
- Manel, S., Williams, H.C., Ormerod, S.J., 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. *J. Appl. Ecol.* 38 (5), 921–931.
- Mann, J., Connor, R.C., Barre, L.M., Heithaus, M.R., 2000. Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. *Behav. Ecol.* 11 (2), 210–219.
- Mayr, E., 1963. *Animal Species and Evolution*. Belknap Press of Harvard University Press, Cambridge, p. 219.
- McNally, R., 2000. Regression and model-building in conservation biology, biogeography and ecology: the distinction between – and reconciliation of – ‘predictive’ and ‘explanatory’ models. *Biodivers. Conserv.* 9, 644–671.
- Mendez, M., 2010. Environmental factors to population structure in mobile marine organisms: a combined genetic-oceanographic approach in coastal cetaceans (Doctoral dissertation), Columbia University.
- Mendez, M., Rosenbaum, H.C., Bordino, P., 2008. Conservation genetics of the franciscana dolphin in Northern Argentina: population structure, by-catch impacts, and management implications. *Conserv. Genet.* 9 (2), 419–435.
- Miller, J., Franklin, J., 2002. Modeling the distribution of four vegetation alliances using generalized linear models and classification trees with spatial dependence. *Ecol. Model.* 157, 227–247.
- Miloslavich, P., Klein, E., Díaz, J.M., Hernandez, C.E., Bigatti, G., Campos, L., Martín, A., 2011. Marine biodiversity in the Atlantic and Pacific coasts of South America: knowledge and gaps. *PLoS One* 6 (1), e14631.
- Monk, J., Ierodiaconou, D., Harvey, E., Rattray, A., Versace, V.L., 2012. Are we predicting the actual or apparent distribution of temperate marine fishes? *PLoS One* 7 (4), e34558.
- Montealegre-Quijano, S., Ferreira, C.N., 2010. Scientific Note Incidental catch of a franciscana dolphin *Pontoporia blainvillei* (Cetacea, Pontoporiidae) in a pair trawl off southern Brazil. *Pan-Amer. J. Aquatic Sci.* 5 (3), 465–468.
- Moreno, M.P.T., 2005. Environmental predictors of bottlenose dolphin distribution and core feeding densities in Galveston bay, Texas (A dissertation submitted to Texas A and M University in partial fulfillment of the requirements for the degree of doctor of philosophy)
- Nix, H.A., 1986. A biogeographic analysis of Australian elapid snakes. In: Longmore, R. (Ed.), *Atlas of Elapid Snakes of Australia*. In: Australian Flora and Fauna Series, vol. 7. Australian Government Publishing Service, Canberra, pp. 4–15.
- Norris, K.S., Dohl, T.P., 1980. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. *Fish. Res.* 77, 821–849.
- Pearce, J., Ferrier, S., 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecol. Model.* 133 (3), 225–245.
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190 (3), 231–259.
- Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31, 161–175.
- Phillips, S.J., Dudík, M., Schapire, R.E., 2004. A maximum entropy approach to species distribution modeling. In: *Proceedings of the Twenty-First International Conference on Machine Learning*. ACM, p. 83.
- Pinedo, M.C., Praderi, R., Brownell, J.R., 1989. Review of the biology and status of the franciscana *Pontoporia blainvillei*. In: Perrin, W.F., Brownell, R.L., Zhou, K., Jiankang, L. (Eds.), *Biology and Conservation of the River Dolphins*. pp. 46–51.
- Polizzi, P.S., Chiodi Boudet, L.N., Romero, M.B., Denuncio, P.E., Rodriguez, D.H., Gerpe, M.S., 2013. Fine scale distribution constrains cadmium accumulation rates in two geographical groups of Franciscana dolphin from Argentina. *Mar. Pollut. Bull.* 72 (1), 41–46.
- Reeves, R., Dalebout, M., Jefferson, T.A., Karkzmariski, L., Laidre, K., O’Corry-Crowe, G., Rojas-Bracho, L., Secchi, E., Sloaten, E., Smith, B.D., Wang, J.Y., Zerbini, A.N., Zhou, K., 2012. *Pontoporia blainvillei*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. [www.iucnredlist.org](http://www.iucnredlist.org) (Downloaded on 10 March 2014).
- Reilly, S.B., 1990. Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. *Mar. Ecol. Prog. Ser.* 66, 1–11.
- Rodriguez, D., Rivero, L., Bastida, R., 2002. Feeding ecology of the franciscana (*Pontoporia blainvillei*) in marine and estuarine waters of Argentina. *LAMAM* 1 (1), 77–94.
- Santos, M.C.D.O., Oshima, J.E.D.F., Silva, E.D., 2009. Sightings of franciscana dolphins (*pontoporia blainvillei*): the discovery of a population in the Paranaguá estuarine complex, Southern Brazil. *Braz. J. Oceanogr.* 57 (1), 57–63.
- Secchi, E., Ott, P., Danilewicz, D., 2003. Effects of fishing bycatch and the conservation status of the franciscana dolphin, *Pontoporia blainvillei*. In: *Books Online*. Vol. 5. pp. 174–191.
- Siciliano, S., 1994. Review of small cetaceans and fishery interactions in coastal waters of Brazil. *Rep. Int. Whaling Comm.* 15, 241–250.
- Siciliano, S., Di Benedetto, A.P., Ramos, R., 2002. A toninha, *Pontoporia blainvillei* (Gervais and d’Orbigny, 1844) (Mammalia, Cetacea, Pontoporiidae), nos Estados do Rio de Janeiro e Espírito Santo, costa sudeste do Brasil: caracterização dos habitats e possíveis fatores de isolamento das populações. *Boletim do Museu Nacional, Nova Série. Zoologia* 146, 1–15.
- Silva, H.S., 2011. Ecologia alimentar da toninha, *Pontoporia blainvillei* (Cetacea) (Dissertação apresentada ao Instituto de Biociências da Universidade de São Paulo Ecologia para obtenção do título de Mestre em Ciências, na Área de Ecologia), São Paulo.
- Smith, B.D., Braulik, C., Strindberg, S., Mansur, R., Diyan, M.A.A., Ahmed, B., 2009. Habitat selection of freshwater dependent cetaceans and the potential effects of declining freshwater flows and sea level rise in waterways of the Sundarbans mangrove forest, Bangladesh. *Aquatic Conserv. Mar. Freshw. Ecosyst.* 19 (2), 209–225.
- Stewart, K.R., Lewison, R.L., Dunn, D.C., Bjorkland, R.H., Kelez, S., Halpin, P.N., Crowder, L.B., 2010. Characterizing fishing effort and spatial extent of coastal fisheries. *PLoS One* 5 (12), e14451.
- Thuiller, W., 2003. BIOMOD—optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biol.* 9 (10), 1353–1362.
- Tsikliras, A.C., Stergiou, K.I., Froese, R., 2013. Editorial note on reproductive biology of fishes. *Acta Ichthyologica Piscatoria* 43 (1), 1–5.
- Valavanis, V.D., Pierce, G.J., Zuur, A.F., Palialexis, A., Saveliev, A., Katara, I., Wang, J., 2008. Modeling of essential fish habitat based on remote sensing, spatial analysis and GIS. In: *Essential Fish Habitat Mapping in the Mediterranean*. Springer, Netherlands, pp. 5–20.
- Viddi, F.A., et al., 2010. Spatial and seasonal variability in cetacean distribution in the fjords of northern Patagonia, Chile. *ICES Mar. Sci.* 67, 959–970.
- Watts, P., Hansen, S., Levigne, D.M., 1993. Models of heat loss by marine mammals: thermoregulation below the zone of irrelevance. *J. Theoret. Biol.* 163 (4), 505–525.
- Wells, R.S., 1987. The social structure of free-ranging bottlenose dolphins. In: Enoways, H.H. (Ed.), *Current Mammalogy*. Vol. 1. Plenum Press, New York, pp. 247–305.
- William, T.M., 1983. Locomotion in the North American mink, a semi-aquatic mammal. I. Swimming energetics and body drag. *J. Exp. Biol.* 103, 155–168.
- Woodward, M., 1999. *Epidemiology: Study Design and Data Analysis*. Chapman and Hall, London.
- Zerbini, A.N., Danilewicz, D., Secchi, E.R., Andriolo, A., Laake, J., 2011. Assessing bias in abundance estimates from aerial surveys to improve conservation of threatened franciscana dolphins: preliminary results from a survey conducted in southern Brazil. IWC Scientific Committee, Tromsø, Norway.
- Zerbini, A.N., Secchi, E.R., Danilewicz, D., Andriolo, A., Laake, J.L., Azevedo, A., 2010. Abundance and distribution of the franciscana (*Pontoporia blainvillei*) in the Franciscana Management Area II (southeastern and southern Brazil). Scientific Committee Document SC/62/SM7. Available from the International Whaling Commission Secretariat, Cambridge, UK.