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REVIEW

Cetacean distribution in relation to environmental parameters between Drake Passage and northern Antarctic Peninsula

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Abstract

The Drake Passage (DP) is a dynamic oceanographic region influenced by the main frontal systems of the Southern Ocean, with little information about cetacean distribution and their relationship with environmental parameters. This study explored the use of generalized additive models (GAMs) to model the relationships of some cetacean species according to sea surface temperature (SST) and a suite of physiographic variables adjacent to the Antarctic Peninsula and DP during the austral summer. The results suggest that SST and distances from oceanographic boundaries, mainly the Southern Antarctic Circumpolar Current Front (SACCF) and Polar Front (PF), were the most significant parameters related to the presence/absence of cetaceans. SST showed an effect on humpback whale (*Megaptera novaeangliae*) presence around lower temperatures and sei whale (*Balaenoptera borealis*) and hourglass dolphin (*Lagenorhynchus cruciger*) at warmer waters. Four species of baleen whales prefer areas near SACCF and Elephant Island and two odontocetes in waters near the PF. Clustering analysis reflected three major groupings based on distances from oceanic fronts and coast: cetaceans that occurred in the northern sector of the DP but with the PF as the southernmost range; a second group with species occurring along the DP and not preferring Antarctic waters further south of the SACCF; and the third group, mainly baleen whales, mostly occupying Antarctic waters southern of the SACCF. We encourage further dedicated cetacean surveys in this particular dynamic region, based on in situ oceanographic data and krill acoustic sampling, and either taking into consideration cetacean species density or abundance.

Keywords Drake passage · Cetacean · Distribution · Antarctica peninsula · Oceanographic parameters · Southern ocean

Introduction

In spite of the Southern Ocean having long been considered a relatively simple marine ecosystem (Knox 2006), the biological and environmental processes determining the abundance and distribution of quite a few species of marine mammals, particularly cetaceans, are still unclear (Nicol et al. 2008; MacLeod 2009; Hays et al. 2016). Although this megafauna is one of the most conspicuous features of the Antarctic marine ecosystem, it is also among the least known, a characteristic that holds true for Antarctica and the Southern Ocean in general (Ducklow et al. 2012).

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The Antarctic Peninsula (AP) is the northernmost part of the Antarctica continent and is a biologically rich area supporting large standing stocks of krill and top predators (including whales, seals and seabirds). Physical forcing greatly affects productivity, recruitment, survival and distribution of krill in this area (Friedlaender et al. 2006; Atkinson et al. 2017) and consequently its predators. The AP is experiencing one of the fastest warming rates on Earth since at least the early 1950s (Ducklow et al. 2012; Friedl et al. 2018), with a concurrent 0.6° increase in temperature of the upper 300 m of the water column (Turner et al. 2014).

The Drake Passage (DP), a strait connecting South America (SA) and the AP, is a very dynamic oceanographic region dominated by the main frontal system of the Southern Ocean, the Antarctic Circumpolar Current (ACC) consisting of the Polar Front (PF), the Subantarctic Front (SAF), the Southern ACC Front (SACCF) and the Southern Boundary of the ACC (SACCB) (Orsi et al. 1995). Particularly, the SACCF is an important ecological feature in this region, influencing mesoscale structure and the distribution from primary production up to top predators (Atkinson et al. 2008; Bost et al. 2009; Santora et al. 2014). Furthermore, the distance interval between those fronts necessarily decreases along the DP since it is the narrowest zone crossed by the fronts (Fig. 1). In the DP waters, scarce information is available about cetacean distribution (e.g. Aguayo-Lobo 1994b; Aguayo-Lobo et al. 1998a, b; Williams et al. 2006; Aguayo-Lobo 2008). Aside from some modelling studies for three baleen whale species (Hedley et al. 2001; Williams et al. 2006; Santora et al. 2010), and some surveys of baleen and toothed whales distribution (Joiris 1991; Kasamatsu et al. 2000; Leaper et al. 2000; Branch and Butterworth 2001; Santora and Veit 2013; Viquerat and Herr 2017), there have been few published studies of cetacean species density, abundance or distribution in relation to environmental parameters in this particular area of the Southern Ocean and more recently an increase in important studies though for the southern region of the DP (Santora and Veit 2013; Santora et al. 2014; Herr et al. 2016), principally due to the rough seas, high seasonality, distances from home ports and land, and the high cost and logistical demands of running multidisciplinary surveys in the Southern Ocean.

From the year 2000 on, one of the leading goals of the International Whaling Commission (IWC) collaborative research in the Antarctic has been to investigate how spatial and temporal variability in the physical and biological environment influences cetaceans (IWC 2000). There has been a growing interest in the integration of biological and environmental data, as many species distributions are defined by interactions between environmental conditions and the ecological niches that they occupy (e.g. Murphy et al. 2007; Whitehead et al. 2008; MacLeod 2009; Hays et al. 2016). Moreover, in recent years an important area of investigation in the Southern Ocean is focusing on the interactions between whales and krill (IWC, 2018), whilst population fluctuations of cetaceans, as top predators, appear to play an important role in past and present changes seen in the Antarctic marine ecosystem (Ainley et al. 2010). Such studies are extremely relevant since accurate information on the distribution of marine mammals is critical to understanding their role in a region's ecosystem (Gedamke and Robinson 2010), and modelling is an important component

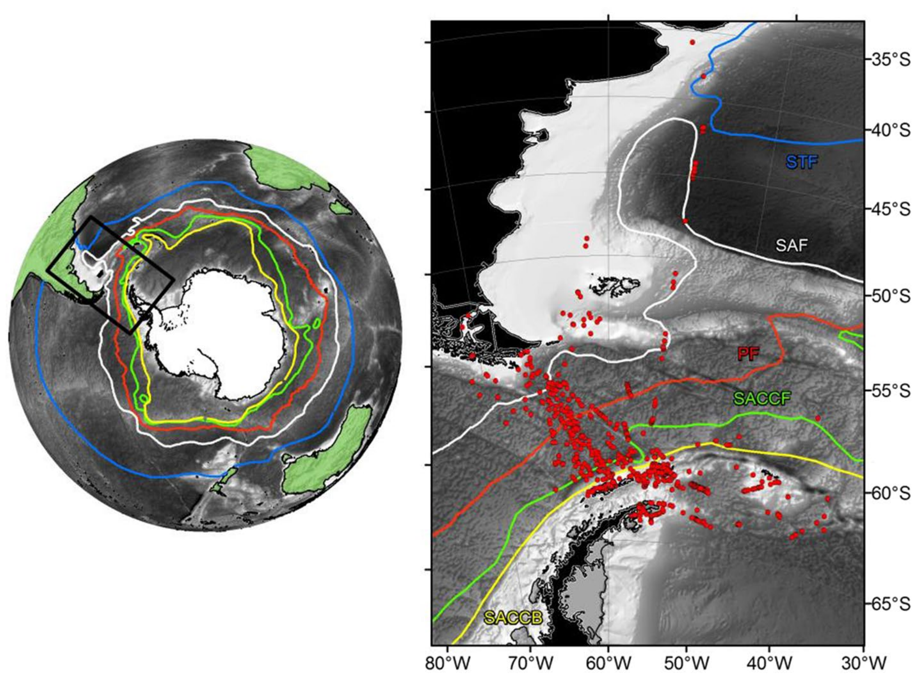

Fig. 1 Map of the research area and cetacean sightings. The map shows the main southern oceanic fronts: Polar Front (PF), Subantarctic Front (SAF), Southern Antarctic Circumpolar Current Front (SACCF) and the Southern Boundary of the ACC (SACCB)

of understanding the interaction of cetaceans and the environment, including conservation implications.

The primary goal of this study is to describe habitat preference and distribution of cetacean species in the DP and northern AP, in particular the north-western region, together with the examination of the effects of environmental variables using data derived from systematic and non-systematic surveys and remote sensing.

We hypothesize that the distribution of different cetacean species could vary in relation to some parameters such as sea surface temperature and oceanographic boundaries, depth, topographic features and distances from land.

Materials and methods

Cetacean sighting data

Data on cetacean distribution were obtained during visual surveys conducted by Brazil (*Programa Antártico Brasileiro*, PROANTAR) for 13 summer seasons (1997–2010) and Chile (*Instituto Antártico Chileno*, INACH) from 1992 to 2010. Dedicated surveys conducted by both countries were mostly focused on the Bransfield and Gerlache Straits (Aguayo-Lobo et al. 1998a, b; Acevedo et al. 2008; Dalla Rosa 2010; Secchi et al. 2001, 2011) but are not included in this study. We based our analysis on the sightings gathered during transits between AP and SA and vice versa, and whenever the vessels transited between dedicated surveys and multidisciplinary research sites. In general, the surveys occurred between November and April, but the data are mostly from December to February (84%).

The visual surveys were conducted by trained observers using standard line transect theory (Buckland et al. 1993). Searching efforts were carried out only in favourable weather conditions (Beaufort = < 4 and visibility > 3 nm). Port and starboard observers used hand-held 7 × 50 binoculars scanning from the trackline to 90 degrees on their side. For each cetacean sighting, a best-estimate spatial position, bearing and a perpendicular distance estimate to the ship's trackline were logged. Where species identification could not be confirmed, higher taxonomic categories were used. In addition, the "minke whale" category was created for the minke whale sightings, as in many cases it was difficult to determine whether it was *Balaenoptera acutorostrata* spp. (dwarf form) or *B. bonaerensis* (Antarctic minke whale), since the dwarf form has been documented in southern SA and around AP (Acevedo et al. 2006, 2011). In the "killer whale" category, we grouped the ecotypes A, B and D (Pitman and Ensor 2003; Pitman et al. 2007, 2011). Additionally, sighting data of published literature from previous years were also included (Chilean database, 1903–1989), mainly related to the DP region (Fig. 1).

It is recognized that such data could not provide analysis aimed at estimating density or abundance. The motivation for analysing these data was mostly to provide insights into cetacean–habitat relationships for some Antarctic and subantarctic areas where scarce information is available (e.g. DP).

Oceanographic and environmental data

A geographical information system (GIS, ESRI ArcGIS, version 10.4) was used to analyse spatial associations between the location of the cetacean sightings and a suite of variables. In this study, we used two types of variables: (i) remotely sensed variables, with sea surface temperature (SST) characterizing the thermal environment; and (ii) physiographic variables such as the bathymetry, topographic features (categorical), distances from land and fronts. SST data were obtained from the AVHRR (advanced very high resolution radiometer) images derived from the MCSST (Multi-Channel Sea Surface Temperature) Programme, since 1981. The spatial resolution was 9 km × 9 km with 8-day averaged temporal resolution, and the claimed accuracy of the MCSST estimate was 0.5 °C. Bathymetric data were extracted from ETOPO2v2 (2-min resolution) database and also used to define the geomorphologic features (deep shelf, shelf, slope, trough, abyssal) according to an Antarctic-wide geomorphic map (O'Brien et al. 2009). Distances from major oceanic fronts and land were calculated as separate variables using a spatial join in ArcGIS to give the shortest distance in metres. The oceanic fronts considered were the PF, SAF, SACCF and the SACCB (Fig. 2). The shortest distances from SA, AP, South Shetlands (SS) and Elephant Island (Elephant) were measured for the analysis. Therefore, all the parameters were linked with the corresponding geographical position and time of each cetacean sighting (interpolated grids from sampling variables). However, for the past literature database (1903–1989) only physiographic variables could be gauged.

Statistical analysis

Clustering

Hierarchical cluster analysis (HCA) on the agglomerative matrices was employed to investigate habitat similarities between cetacean species according to distances from selected lands (SA, PA and SS) and major oceanic fronts (PF, SAF, SACCF and SACCB). For this analysis, the species with at least ten sighting events were included, and they are: hourglass dolphin (*Lagenorhynchus cruciger*), Peale's dolphin (*Lagenorhynchus australis*), southern right whale dolphin (*Lissodelphis peronii*), humpback whale (*Megaptera novaeangliae*), minke whale,

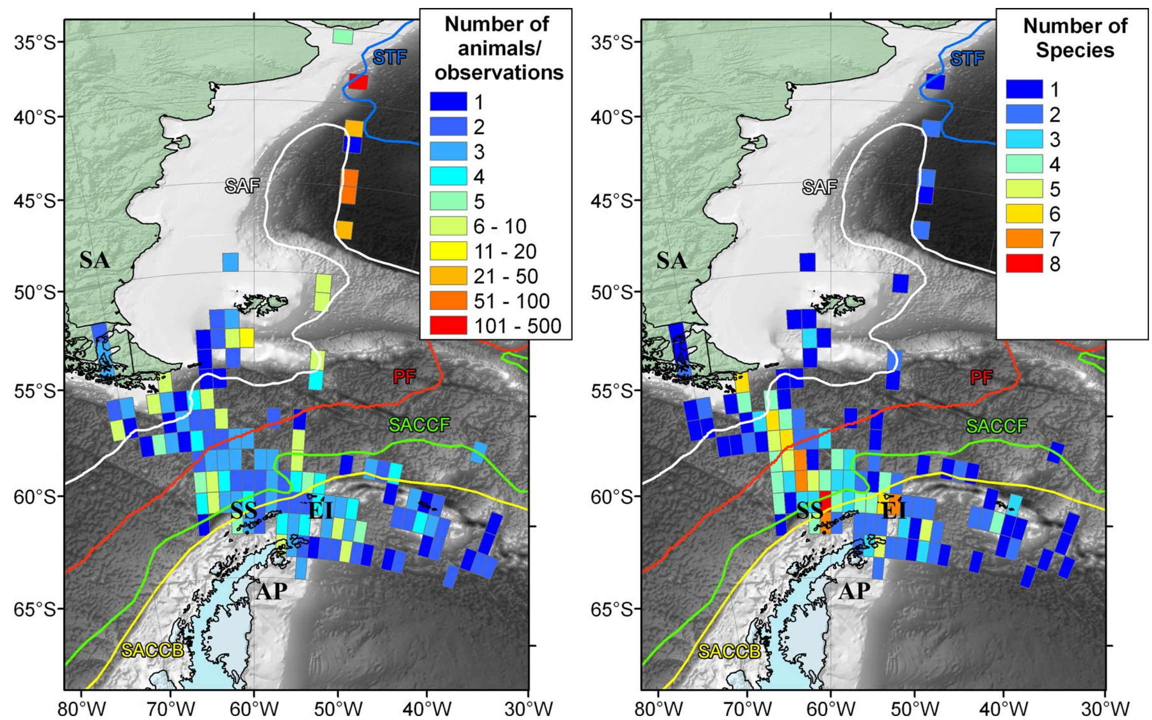

Fig. 2 Map of the research area gridded to 30-min square (35°S to 65°S), with all cetacean sightings according to the number of animals (left graph) and the number of species (right graph). The oceanic fronts: Polar Front (PF), Subantarctic Front (SAF), Southern Antarctic Circumpolar Current Front (SACCF) and the Southern Boundary of the ACC (SACCB). Land and coasts: South America (SA), Antarctic Peninsula (AP), South Shetlands (SS) and Elephant Island (EI)

sei whale (*Balaenoptera borealis*), fin whale (*Balaenoptera physalus*), killer whale (*Orcinus orca*), sperm whale (*Physeter macrocephalus*), long-finned pilot (*Globicephala melas*), southern right whale (*Eubalaena australis*) and the southern bottlenose whale (*Hyperoodon planifrons*). The research area contemplated for the clustering ranged from 41°S to 65°S (Fig. 3).

HCA was calculated using the *Manhattan* distance and Ward's minimum variance method, using the "factoextra" package (Kassambara and Mundt 2016) in the R statistical environment (R Development Core Team 2018). The variables were scaled (i.e. standardized) before measuring the inter-observation dissimilarities. The shorter the distance, the more similar the measures and the more likely the species involved will be included in a group. *Manhattan* was chosen because large differences in a single index will not have as large an impact on final similarities as with the Euclidean distance and it works better for high-dimensional vectors (Kassambara 2017), and Ward's minimum variance method avoids distortion (Murtagh and Legendre 2014). HCA produced a tree-based representation (dendrogram), indicating groups of cetacean species sharing similar habitat. We used several analytical tools to identify the optimal arrangement of species among groups, including visual inspection of the dendrograms, inspect cophenetic and original distances correlation, bootstrap resampling and successive cluster configurations.

Generalized additive models (GAMs)

The study area (55°S to 65°S) was gridded to 30-min square, covering the cetacean sightings mainly for the region between SA and AP (Fig. 4). The sighting data were grouped for each 30-min box grid, as well the spatial resolution of the oceanographic and physical parameters, determined by the pixelation in the data stored in GIS. Only the grids with sighting data were taken into account for the models as the presence of a determined species was used as an indication of effort that did not record the presence of other species. Temporal resolution included only the sightings of summer months (December to February). Additionally, only eight species with higher numbers of observations were taken into account as response variables: humpback whale, minke whale, sei whale, fin whale, killer whale, long-finned pilot whale, southern bottlenose whale and the hourglass dolphin. The suite of predictor variables included those related to the physiographic variables: water depth, topographic feature, distances from coasts and fronts and the oceanographic parameter SST. Pairwise comparison of all covariates and variance inflation factors (VIF) was applied

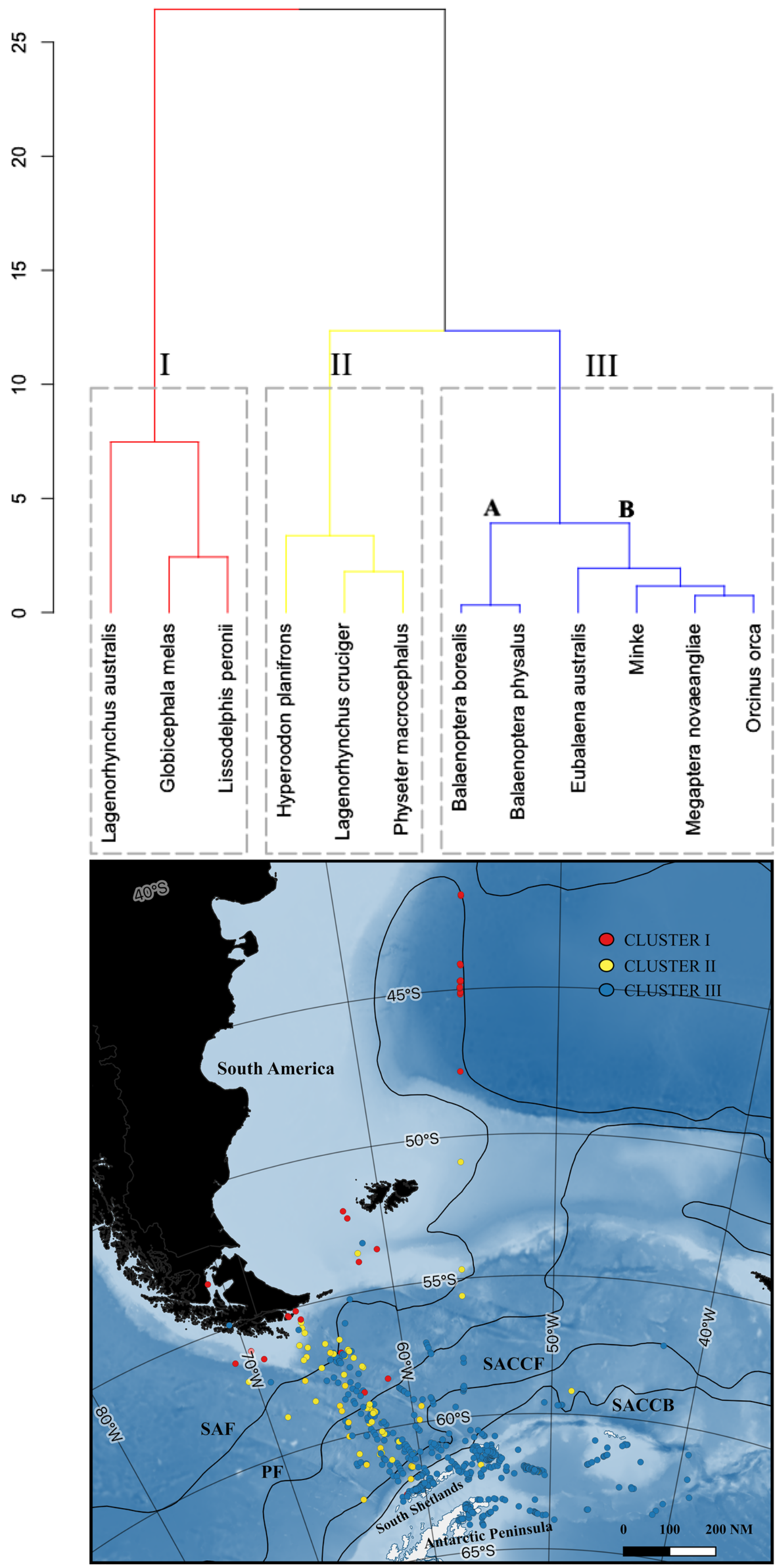

Fig. 3 Clustered display of cetacean species correlated with minimum distances from land (South America, Antarctic Peninsula and South Shetland Islands) and fronts (SAF, PF, SACCF and SACCB), during austral summer months

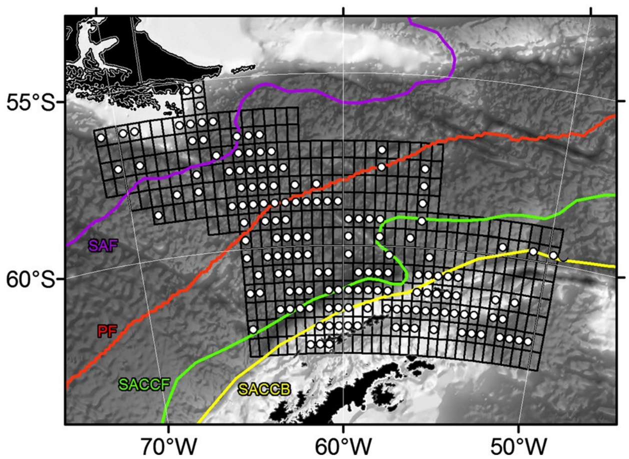

Fig. 4 Study area considered for the GAM analysis gridded to 30-min square (55°S to 65°S), with the point location for the grids with cetacean sightings data

to detect correlation and multicollinearity (Zuur et al. 2009), and only the predictors with no effects of collinearity were chosen for the models (Table 1).

In order to represent distribution as realistically as possible for the data, GAMs were used both considering presence and pseudo-absence data for each species. The pseudo-absences were generated from the sightings of all species other than the key species. The observation of other species was used as an indication of effort that positively did not record the presence of the target species (as the protocols usually record all observed species in the area). The presence of a species was classified as either 1 (at least one sighting) or 0 (no sighting).

The models were built to integrate biological and physical data within a generalized additive modelling framework using the "mgcv" package (Wood 2004, 2006) in the R statistical environment (R Development Core Team 2018). Response variables measuring presence and pseudo-absence for each cetacean species were analysed with GAM based on a binomial family (logit link) model structure, as the errors are expected to be highly skewed because of many zeros in the data (cetacean absence), and provided an alternative of modelling allowing for overdispersion (Venables and Ripley 1997). The model was specified as cetacean species ~ s(SST) + s(Depth) + s(PF) + s(SACCF) + s(Elephant) + Topo, where smoothing function s() denotes regression splines. Model sel ection was based on restricted maximum likelihood (REML) score, and final models included only those predictors whose deviance reduction was significant at the 0.05 confidence level (p value). The per cent change in deviance between the final model and the null model was calculated as a measure of the amount of variation explained by the model (deviance explained), and together with the adjusted R^2, we can evaluate model performance. The effect of each covariate included in the GAM was plotted (Fig. 5) to visually inspect the functional form of cetaceans' occurrence in relation to significant covariates during austral summer months in the study area (Fig. 4).

Results

A total of 955 sightings of cetaceans (4650 animals and 1098 groups) were recorded (Fig. 1). Humpback whales were most often sighted, followed by minke and fin whales. Hourglass dolphin, southern bottlenose whale, killer whale and long-finned pilot whale were the odontocete species with higher school numbers. A summary of the sightings, oceanographic and physical parameters range and topography for all the cetaceans is presented in Table 2.

Clustering

According to habitat similarities, in terms of distances from land and fronts, three major cluster groups could be defined for several cetacean species in the study area during summertime (Fig. 3). Group I is composed of cetaceans that

Table 1 The unit of measure, transformation and sampling method for each predictor variable used in GAMs of cetacean presence patterns

Parameter	Explanation	Units	Transformation	Sampling method	Acronyms
Water temperature	Mean of weekly SST	°C	None	Interpolated grids from sampling variables	SST
Bathymetry	Water depth of the sighting	m	None	ETOPO2	Depth
Topographic features	Shelf, Slope, Deep shelf, Trough, Abyssal	None	None	ETOPO2/O'Brien 2009	Topo
Land distances	Species sighting minimum distance from South America and Elephant Island	m	km	Straight line distance sightings/grids	AS Elephant
Front distances	Species sighting minimum distance from Polar Front and Southern Antarctic Circumpolar Current Front	m	km	Straight line distance sightings/grids	PF SACCF

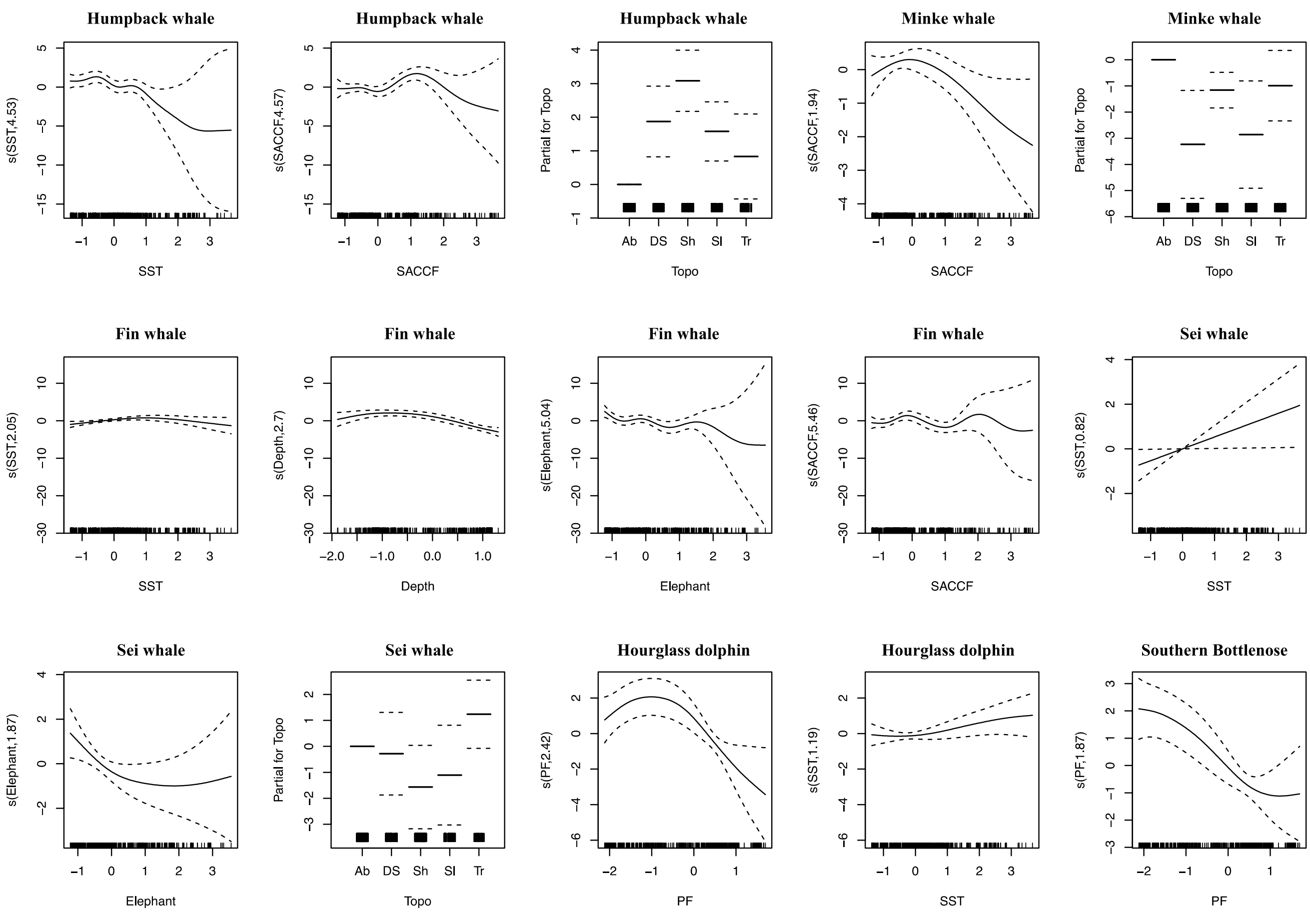

Fig. 5 Generalized additive model functions for humpback whale, minke whale, fin whale, sei whale, hourglass dolphin and southern bottlenose whale sightings in relation to oceanographic and environmental variables. Continuous lines indicate the estimated smooth terms; dashed lines indicate the 95% confidence limits; x-axis indicates the explanatory variable and y-axis fitted the smooth function with the estimated degrees of freedom (*Ab* abyssal, *DS* deep shelf, *Sh* shelf, *Sl* slope, *Tr* trough)

occurred along the DP but with the PF as the southernmost range. Group II is the species frequently occurring along the DP, hence not preferring Antarctic waters further south the SACCF. Group III is described as the species occurring frequently in the DP and Antarctic waters southern of SACCF and SACCB, composed of both offshore species (subgroup A) and species mostly preferring coastal areas and straits (subgroup B).

GAMs

GAMs results (Table 3) suggest that distances from oceanic fronts and SST were the most significant parameters related to the presence–absence of cetacean species in the study area during the austral summer. Except for one explanatory variable (distance to SA), all other covariates were significant in the analysis. No interaction terms were preferred according to model selection (residuals and significance testing, REM scores).

The model for humpback whales across the spatial grids suggests higher presence of this species in the shelf and deep shelf, and the smooth function for SST showed a positive effect on humpback whale presence around lower temperatures decreasing towards higher values (Fig. 5). Likewise, it seems that at closer distances from SACCB there were more incidences of humpbacks. The explanatory power of the model was moderate, with the deviance explained 33% and the adjusted R^2 score was 0.37 (Table 3). There are four significant predictors influencing the presence of fin whale, with higher presence of this species near Elephant and the front SACCF, and a quadratic relationship with SST and depth (36% of explained deviance). The occurrence of minke whales is higher at close distances from SACCF and over the continental shelf. As for humpback whales, the SST seems to influence the presence of sei whales, though this species appears more frequently in warmer waters with a positive relationship of its occurrence closer to Elephant (Fig. 5). However,

Table 2 Total cetacean sightings (individual sightings and schools) and physical variables range, from Brazilian and Chilean surveys

Species	Common name	Schools	Indiv	SST (°C)			Water depth (m)			Topography
				Min	Mean	Max	Min	Mean	Max	Most frequent
Mysticetes										
Balaenoptera musculus	Blue whale	1	1					3451		Slope
Balaenoptera physalus[a,b]	Fin whale	113	321	− 2.78	1.24	6.90	99	2549	4469	Abyssal/Deep Shelf
Balaenoptera borealis[a,b]	Sei whale	46	115	− 2.90	0.90	8.40	128	2463	4911	Abyssal
Minke whale[a,b]	Minke whale	183	364	− 2.90	− 0.19	6.83	10	1919	5195	Shelf
Megaptera novaeangliae[a,b]	Humpback whale	364	783	− 2.85	− 0.70	2.70	19	950	4971	Shelf
Eubalaena australis[a]	Southern right whale	11	17	− 2.63	− 0.34	2.02	19	980	3131	Shelf
Balaenoptera sp.	Rorqual whale	13	27	− 2.78	0.71	6.68	19	2666	4557	Abyssal
Total		731	1628							
Odontocetes										
Physeter macrocephalus[a]	Sperm whale	4	5		0.08		587	2172	3738	Slope
Orcinus orca[a]	Killer whale	40	261	− 2.85	0.27	8.18	19	875	4961	Shelf/Deep shelf
Globicephala melas[a]	Long-finned pilot whale	41	1,055	− 1.80	10.39	14.12	110	4501	5720	Abyssal
Lissodelphis peronii[a]	Southern right whale dolphin	10	451	10.14	12.96	14.04	4539	5411	5705	Abyssal
Lagenorhynchus australis[a]	Peal's dolphin	11	41	6.68	8.69	9.68	4	449	3059	Shelf
Lagenorhynchus cruciger[a,b]	Hourglass dolphin	37	229	− 2.78	2.95	7.95	77	3322	4291	Abyssal
Lagenorhynchus obscurus	Dusky dolphin	1	6		6.70			10		Shelf
Cephalorhynchus commersonii	Commerson's dolphin	7	26	3.30	5.25	7.88	32	2569	3970	Abyssal
Cephalorhynchus eutropia	Chilean dolphin	1	3		− 2.85			4014		Abyssal
Delphinus delphis	Common dolphin	10	500		20.29			906		Slope
Tursiops truncatus	Bottlenose dolphin	1	10		14.12			5222		Abyssal
Hyperoodon planifrons[a,b]	Southern bottlenose whale	22	40	− 0.96	2.33	6.39	1794	3710	4258	Abyssal
Berardius arnuxii	Arnoux's beaked whale	2	3	6.00	6.71	7.42	3590	3642	3694	Abyssal
Ziphius cavirostris	Cuvier's beaked whale	2	3	− 0.53	0.30	1.13	3345	3573	3801	Abyssal/trough
Ziphiidae[a]	Beaked whale	14	24	− 2.85	1.01	5.77	543	3015	4543	Abyssal
Lagenorhynchus sp.	dolphin	12	59	− 2.78	2.68	5.25	7	906	3845	Shelf
Mesoplodon sp.	Beaked whale	2	5	6.52	7.01	7.50	3006	3662	4319	Abyssal
Total		217	2721							
Unidentified		150	301							

The variable values considered are for the smaller spatial resolution (9 km for SST and 2-min resolution for depth and topography)

[a]Cetacean species considered for clustering

[b]Cetacean species considered for the GAM analysis

Table 3 Summarized results of GAM analysis of association between selected cetacean species and environmental variables, using REML (restricted maximum likelihood) score

Family = binomial (link = logit)	Covariates	Est. df	χ^2	*p* value
Humpback whale	s(SST)	4.53	23.88	< 0.0001
	s(SACCF)	4.57	23.33	< 0.0001
	Topo	4.00	48.66	< 0.0001
Performance	R^2 adj. = 0.37, deviance explained (%) = 33.0, REML score = 280.02			
Fin whale	s(SST)	2.05	9.06	0.0053
	s(Depth)	2.70	38.69	< 0.0001
	s(Elephant)	5.04	21.32	< 0.0001
	s(SACCF)	5.46	19.70	0.0002
Performance	R^2 adj. = 0.35, deviance explained (%) = 36.2, REML score = 173.66			
Sei whale	s(SST)	0.82	4.29	0.0191
	s(Elephant)	1.87	6.26	0.0191
	Topo	4.00	13.68	0.0079
Performance	R^2 adj. = 0.05, deviance explained (%) = 13.0, REML score = 98.74			
Minke whale	s(SACCF)	1.94	6.89	0.0185
	Topo	4.00	24.73	< 0.0001
Performance	R^2 adj. = 0.06, deviance explained (%) = 10.6, REML score = 188.59			
Hourglass dolphin	s(SST)	1.19	3.70	0.0429
	s(PF)	2.42	16.99	< 0.0001
Performance	R^2 adj. = 0.08, deviance explained (%) = 20.1, REML score = 91.53			
Southern bottlenose whale	s(PF)	1.87	18.56	< 0.0001
Performance	R^2 adj. = 0.45, deviance explained (%) = 15.9, REML score = 71.14			

For the explanatory variables, only the significant *p* values are shown. The variable values considered are for the gridded spatial resolution (30 min)

Est. df estimated degrees of freedom, χ^2 = chi-square test, R^2 *adj.* adjusted R^2

the explanatory power of the model was not great for either minke or sei whales (Table 3). For odontocetes, the best fitting resulted in only two significant explanatory parameters. SST and distance from PF were selected in the GAM for hourglass dolphin (Table 3). The presence of this species appears to be influenced by distance from PF, with a strong negative relationship and the covariate explaining most of the deviance in the model and providing great improvement to the fit, followed by a positive relationship of hourglass dolphin with warmer waters. The smooth curve of distance from the PF for southern bottlenose whale model suggests a nonlinear relationship with higher values closer to the front, decreasing its presence towards increasing the distance from the PF, and after the numbers increased again, but also the intervals (Fig. 5).

Discussion

The distribution of cetacean species in relation to habitat in Antarctic waters is likely to be a complex interaction of many factors including currents, ice, bathymetry, oceanography, prey distributions and perhaps behaviour such as avoiding prey competition and predation (Kasamatsu et al. 2000; Friedlaender et al. 2006; Nicol et al. 2008; Orgeira et al. 2015). In this study, the models to analyse cetacean species expected presence according to some environmental variables (depth, bottom topography, distances from lands and fronts and SST) revealed that areas closer to fronts play an important role and were significant drivers of their occurrence. These findings might be strongly linked to foraging, as high productivity areas in Antarctic waters have been found at oceanic fronts or eddies, and areas of upwelling, as marginal shelf and sea ice zone, and coastal areas (e.g. Smith and Nelson 1986; Hoffman et al. 1998; Thiele et al. 2000; Trathan et al. 2007; Bost et al. 2009). Additionally, the Atlantic sector of the Southern Ocean has been confirmed as the area where both the largest concentrations and the highest densities of krill are found (Atkinson et al. 2004, 2017).

GAMs

Baleen whales

The presence of three baleen whales - humpback, minke and fin - were significantly associated with areas near the SACCF, which may be due to frontal processes, such as meanders and eddies, which concentrate prey and enhance foraging potential and success (Santora and Veit 2013; Santora et al. 2014). Fin whale distribution also has been mentioned in terms of a preference for frontal areas both in Antarctic waters (Tynan 1998; Bost et al. 2009) and other oceanic regions (Clarke 1962; Clarke et al. 1978; Hamazaki 2002; Doniol-Valcroze et al. 2007; Laran and Gannier 2008). Hedley et al. (2001) also suggested that fin whales in Antarctic waters are opportunistic feeders and do not rely solely on a diet of krill but also prey on mycthophid fishes, where a major peak in biomass was observed in the vicinity of the PF (Pakhomov et al. 1996). Moreover, fin whales were seen feeding on krill swarms in oceanic waters of DP (A. Atkinson pers. comm.), and Siegel et al. (2004) found that largest mature krill (spawning stock) occurred in a continuous band across the western oceanic waters of DP. Therefore, fin whales presence could be related to adult krill swarms in offshore waters of the DP, possibly closer to SACCF. Santora and Veit (2013) showed that fin whale displayed persistent hotspots that were closely associated with the positions of the SACCF and SACCB. However, the same authors found a negative association of these fronts and humpback whales, the opposite to our findings. However, during surveys in the Scotia Sea most humpback whales were recorded south of 60°S near the SACCF (Orgeira et al. 2015), and both cetacean species, humpback and fin, have been recorded in waters close to SACCF (Reyes Reyes and Iñiguez 2013; Orgeira et al. 2017). GAM analysis of the physical environment associate with Antarctic minke whale density found the closest distance to SACCF covariate most often included in the models (Beekmans et al. 2010). However, these authors suggested that SACCF might not be as important for minke whale as it has been reported to be for other baleen whales (Tynan 1998; Beekmans et al. 2010; Orgeira et al. 2015, 2017).

There was a common effect of distance from Elephant covariate for fin and sei whales occurring at closer distances to this island. For the survey data, in many occasions sei whales were encountered in the same areas as fin and mixed groups were observed, which also occurred in Greenland waters (Heide-Jørgensen et al. 2007). Many studies on krill biomass from the western AP throughout Scotia Sea found high densities of krill (Hoffman et al. 1998; Lascara et al. 1999; Hewitt et al. 2004), and it is clear that north-west of Elephant aggregates important krill biomass (Hewitt and Demer 1993; Siegel et al. 1997, 2002; Atkinson et al. 2017). Higher densities of fin whales nearby northern Elephant were described (Williams et al. 2006), and Santora et al. (2010) study about associating hot spots of baleen whales and krill demographic patterns found fin whale hot spots located north of Elephant.

The findings of this study, which represent similar patterns of others researches, might be related to prey distribution, and the more spread out presence of humpback whales throughout different areas than the other baleen species could be associated with the predation of different size classes of krill among whale species as suggested by Santora et al. (2010). Other studies also found different size classes of krill spatially segregated along the western AP (Siegel et al. 1997; Hoffman et al. 1998). Humpback whales tended to aggregate over areas of small krill swarms, whereas fin whales aggregated over large krill swarms and minke whales overlapped intermediate size of krill swarms (Santora et al. 2010). It is not clear whether these three whale species select size class swarms of krill, probably related to their distinct filter feeding apparatus (Aguayo-Lobo et al. 1993), or choose particular habitats, or depth foraging (Friedlaender et al. 2015), to minimize competition. Recent studies in the DP and west of AP suggest that fin whales feed primarily on *Thysanoessa macrura* and humpback whales on *Euphausia superba* (Herr et al. 2016), which could be another strategy to reduce prey competition.

Humpback whale

The presence of humpback whales in this research was higher in relatively colder sea surface waters, which corroborates with other studies (e.g. Nicol et al. 2000; Orgeira et al. 2017). This pattern reflects the distribution of humpback whales from historical catch records (Mizroch et al. 1985). Furthermore, Kasamatsu et al. (2000) found the highest density of these whales in Antarctica within waters between −1.0 and 0.5 °C. Topography was an important covariate in the model, with higher presence of this baleen whale in shelf areas. The findings of some studies are either associating humpback distribution along closest areas of the western side of the AP (Hedley et al. 2001; Williams et al. 2006; Dalla Rosa 2010), increasing proximity to shore over the foraging season (Curtice et al. 2015), or at shallower areas in the southern Scotia Sea (Orgeira et al. 2017).

Minke whale

Murase et al. (2002) suggested that minke whales in Antarctic waters concentrate in areas where the continental slope, shelf and the ice edge are coincident. Similarly, Kasamatsu et al. (2000) and Santora et al. (2010) showed higher densities of minke whales in waters over the shelf and shelf break, and Thiele et al. (2004) found these whales in great numbers over the shelf. The findings of this study also suggest high occurrence of minke whales over the shelf and slope areas. Moreover, ice edge or marginal ice zone might be an important factor controlling the occurrence of minke whales (Aguayo-Lobo 1994a; Kasamatsu et al. 2000; Friedlaender et al. 2006; Ainley et al. 2007), which was not considered in our models.

Fin whale

Depth is a significant covariate, with higher presence of the species far from shallow and shelf waters. Kasamatsu et al. (2000) suggested that the species tended to be distributed in the deep-sea area, and Williams et al. (2006) predicted higher densities of fin whales in offshore waters, running parallel to the AP. According to our results, the presence of fin whale was also higher for warmer SST. Ship survey, heading south of 61°S, recorded an SST increasing from 0.4 to 1.4 °C together with an increase in fin whale sightings (Orgeira et al. 2017). However, the increase in SST probably corresponds to marine fronts or eddies; hence, the presence of fin whales in warmer waters might be linked to oceanic fronts boundary, which was discussed earlier as an important covariate for the presence of fin whales.

Sei whale

There are very limited information of sei whale distribution for the study area and no information relating the species with environmental variables except presence of sei whale in the Magellan Strait (Acevedo et al. 2017b). There is a significant relationship of sei whale presence within warmer temperatures in this study, jointly with sightings from other survey studies (e.g. Hedley et al. 2001; Williams et al. 2006). Such findings suggest the region as the edge of its southern range facilitated sometimes by discrete increases of water temperature during austral summer. MacLeod (2009) discusses the temperature range of sei whale as a warmer-water limited species but with ability to occur in cooler waters at the higher latitude edge of their ranges. Topography also plays an important role for sei whale presence in deeper areas (trough and abyssal), corroborating with the results of clustering, where together with fin whales they occupy offshore waters of Group III.

Odontocetes

Hourglass dolphin, southern bottlenose whale, killer whale and the long-finned pilot whale were the most sighted odontocetes in this study, corroborating with other survey studies in Antarctica (Joiris 1991; Kasamatsu and Joyce 1995; Williams et al. 2006). The hourglass dolphin showed a significant relationship with areas closer to PF and warmer waters. Kasamatsu and Joyce (1995) found the species mainly occurred in the northernmost areas of the Antarctic, especially in the South Atlantic sector. Conversely the hourglass dolphin seems to avoid shelf areas, which was sighted several times in the shelf closer to the Beagle channel in this study. MacLeod (2009) categorized the hourglass dolphin as “primarily oceanic”, and Goodall (1997) also suggested this dolphin habitat as pelagic and ranging mostly between 45 and 60°S. Recently, the first sight of this species in inland waters of southern Chile (Parry fjord) was reported, suggesting some environmental shift within DP affecting the movements of the dolphin to north of PF (Acevedo et al. 2017a). The southern bottlenose whale showed high presence nearby the PF. These results are in agreement with the findings of Kasamatsu and Joyce (1995) with high encounter rates between 58°S and 62°S, appearing to have a wide distribution between the Antarctic convergence and the pack ice edge, mainly near the shelf slope or in epipelagic waters (Santora and Brown 2010).

Clustering

Studies describing patterns for seabird species distribution across DP have quantified five distinct species assemblages that correspond to biogeographical regions and relate to the positions of the SAF, PF and SACCF (Force et al. 2015). Clustering our data according to distances from these oceanic fronts, we also found distinct cetacean groups throughout the DP (Fig. 3). Group I belongs to only odontocetes that occupy areas closer to SAF and further north, with few observations north of PF. Group II is odontocetes that prefer a biogeographical zone between SAF and SACCF, with two species significantly associated with PF (Table 3). All the baleen whales and killer whale belong to Group III, also occurring along the DP, but occupying mostly waters under the SACCF, with killer, minke and humpback whales mostly occupying coastal areas, whereas fin and sei whales preferring offshore waters. Similar to our findings, Santora and Veit (2013) described clustering top predator abundance off the AP revealed fin whale in the offshore group and humpback whale in the coastal zone assemblage, and this species has generally been described as occurring further to the north of blue, humpback and minke whales in Antarctic waters (Hedley et al. 2001; Gedamke and Robinson 2010; Orgeira et al. 2015). The separation of the major southern oceanic fronts, each with distinct temperature, salinity and stratification characteristics, imposes ecological zonation not only for the study area (DP) but for the entire Southern Ocean (Pollard et al. 2002; Venables et al. 2012). Undoubtedly, cetacean species habitats reflect physical characteristics of the hydrographic fronts in the Southern Ocean. Many species assemblages’ distribution ultimately reflects evolutionary development associated with the persistence of these fronts and biogeographic zonation across DP (Force et al. 2015).

Data limitation and recommendations

Our SST results could be underestimated since it was not possible to join values for all the sightings (null values) as these data depend on satellite images, which sometimes were not available due to weather conditions (e.g. cloud cover). Unfortunately, it was not possible to obtain two important predictors for our models, sea ice (marginal zone distance) and krill density data. We believe that sea ice should be an important predictor in our models (for AP region) because many whales exhibit life histories with affinities to sea ice, whilst the other known species tend to be ice avoiding (Pitman and Ensor 2003; Širović et al. 2004; Ainley et al. 2007; Nicol et al. 2008). Krill density data for most of the study area and timescale were not available.

The GAM approach is used widely to understand species presence and absence patterns (Ward 2007; Laidre et al. 2010; Virgili et al. 2017), though its flexibility can potentially lead to the over-fitting of data and as such precaution must be considered in the light of the explanatory power of the models. The best fitting models explained no more than 36% of the deviance, which suggests that other more important explanatory variables were missing in the models (e.g. distance of ice edge) and the more obvious would be the prey distribution, mainly the krill. There are drawbacks associated with the spatial and temporal scales of analysis. Our study was restricted to about 50% of cetacean presence cells in the designed gridded area (Fig. 4), and this could bias our results because many gridded areas were not taken into account in the models. Moreover, we did not take into account inter-annual variability in the models (unbalanced factor levels), which might play an important role to be considered in further analysis with more years added and a balanced design. Krill distribution and density vary significantly over years, within high inter-annual variability of krill recruitment (see Siegel et al. 1997; Lascara et al. 1999; Murphy et al. 2007). Consequently, marked seasonal and inter-annual variability in this environment over years apparently affects cetacean distribution (Thiele et al. 2004; Trathan et al. 2007; Dalla Rosa 2010; Friedlaender et al. 2011).

The results presented here should be viewed as an important initial effort because they portray cetacean presence according to environmental variables for some areas with little information available. This approach provides valuable information for some cetacean species presence, mainly odontocetes and their correlation with environmental parameters between SA and AP, and its adjacencies.

Further studies should consider a dedicated and well-designed cetacean survey between SA and AP, preferentially based on in situ oceanographic data (e.g. CTD) and krill acoustic sampling, which allows improving the explanatory variables modelling, and either taking into consideration cetacean species density or abundance. Sea ice cover data from remotely sensed imagery should be contemplated for future analysis of cetacean surveys in the AP, likewise chlorophyll *a* (Chl*a*) data. Some studies propose significant influence of Chl*a* concentration and whale density (see Laran and Gannier 2008; Loeb et al. 2009; Dalla Rosa 2010). We believe that more data are required to better understand these cetacean–oceanographic parameter interactions in the study area. Understanding the interactions between oceanographic features and top predators dynamics in rapidly changing marine environments, like the DP and AP, is critical to predicting the impacts on climate-driven changes to these ecosystems.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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